Walleye (*Sander vitreus*) movement ecology in Lake Winnipeg, Canada

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Abstract

Identifying differences in movement behaviour and the variance in behavioural strategies that may exist across a single species occupying a heterogeneous landscape can provide valuable ecological and evolutionary insights; taking movement heterogeneity into account in management and conservation efforts may ultimately improve the sustainability of species with significant economic and ecological value, such as walleye (*Sander vitreus*). Lake Winnipeg (Manitoba, Canada) supports the second largest commercial fishery for walleye in North America. The lake is divided into two relatively separate basins connected by an intermediate channel, which differ dramatically in both abiotic and biotic features. Despite this, little is known about whether (or how) walleye move or use variable habitats throughout the lake.

Historical mark-recapture models from tagged walleye revealed low but measurable rates (0.3-1.2%) of movement annually between the north and south basins of Lake Winnipeg. Contemporary estimates using acoustic telemetry data detected a greater but comparably low rate of transition between the basins annually for walleye (7-8.5%). Both historical and current models revealed that movement was more likely to occur in a south to north direction. Additionally, annual survival across both basins of the lake was higher historically (54%) then it is currently (37%).

To further investigate contemporary patterns of inter-basin movement, I assessed female walleye tagged across the south. I uncovered repeatable patterns of individual fish movement, where migratory walleye consistently travelled into the north basin for a period of time, and resident walleye remained within the south basin. I found that migrants significantly increased home (95%) and core (50%) ranges during the summer and fall associated with a northern shift in latitudinal distribution. Finally, putative repeat spawning in the year following tagging appeared to be greater for migrants (65%) compared to residents (40%). This thesis describes the first formal description of walleye movement in Lake Winnipeg, and suggests connections between movement patterns (i.e., migrants and residents) to potential differences in life history (i.e., differential probability of repeat spawning). Direct movement results presented here should prove useful to fisheries management and policy for both commercial and recreational activities across the separately managed basins of Lake Winnipeg.

Lay Summary

Lake Winnipeg walleye contribute millions of dollars to the province in revenue directly and indirectly related to the commercial and recreational fisheries across the lake. Additionally, walleye provide sustenance and income to many Indigenous communities surrounding the lake. Studies regarding how walleye use differing basins across Lake Winnipeg have focused on genetic and morphological analysis where genetic studies have indicated mixing while morphological studies have found basin specific specialization. This is the first study to measure and track direct movements of walleye while additionally comparing datasets evaluating movement spanning 50 years. To directly measure movement of walleye across Lake Winnipeg, I used a historical mark-recapture study conducted in the 1970's by the Province of Manitoba, as well as a contemporary acoustic telemetry study initiated by Fisheries and Oceans Canada. Major results of this thesis demonstrated that a portion of the tagged populations across the north and south basins both currently and historically used a much larger area of the lake then has been previously thought, migrating into opposite basins of the lake from where they were initially tagged. Furthermore, I demonstrated that a portion of large, female walleye spawning across the south basin of Lake Winnipeg made long distance migratory movements up into the north basin. Additionally, these migratory individuals typically returned to the south basin to spawn the following year at a greater rate than those who remained resident in the south basin, providing some evidence that fish exhibiting migratory behaviour may benefit from increased reproductive output.

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Chapter 1. General Introduction

1.1 Background

Freshwater ecosystems have been exploited for hundreds of years, with the majority of exploitative activities occurring within the past 100 years (Cambary, 2003; Naiman & Turner, 1999). Historically, little attention was paid to the implications and consequences of depleting and degrading freshwater ecosystems and their associated flora and fauna. Reflecting this degradation, predictive models indicate a 4% extinction rate per decade of species in North American freshwater ecosystems (Ricciardi & Rasmussen, 1999). The need for conservation and proper management of these ecosystems and associated species clearly is greater than ever with biodiversity of freshwater ecosystems more imperilled that marine or terrestrial habitats (Díaz et al., 2019). The greatest threats identified currently impacting freshwater systems are: exploitation, pollution, alteration of water flow, habitat degradation, and introduction of invasive species (Cooke & Murchie, 2015; Dudgeon et al., 2005; Richter et al., 1997). As climate change continues to alter current systems in the northern latitudes, freshwater habitats will remain under increased threat (Cooke & Murchie, 2015). If fisheries are not properly managed, they are at an increased risk for both local and broad scale changes that may be irreparable (Cooke & Murchie, 2015). Overharvest through both commercial and recreational activities has the potential to reduce biodiversity while allowing for opportunistic invasive species to move into previously unoccupied areas (Rapport & Whitford, 1999).

Until recently, studying fine scale movements of fish and various aquatic species, both marine and freshwater proved challenging. However, with the development of new bioacoustics and satellite technologies, possibilities for tracking the movement of aquatic animals has improved dramatically (Cooke et al., 2004; Priede & Swift, 1995). These technologies have revealed significant insights into the timing of movement between various habitats for many species that have proved useful in both successful management and conservation. For example across Lake Huron acoustic telemetry results contributed to fishery management and policy in regards to total harvest limits on walleye populations (Hayden et al., 2014; Krueger et al., 2018). Subsequently, this information can be used to aid fisheries managers or other decision-makers when developing regulations that will improve management strategies to better ensure the sustainability and conservation of species at risk, and species that are targeted by commercial fisheries, recreational fisheries, or both.

Lake Winnipeg

Lake Winnipeg is the 11th largest freshwater lake in the world and the third largest lake fully within Canadian borders, with a total surface area of 23,750 km^2 (Brunkskill et al., 1980). However, the lake is poorly represented in the scientific literature; fewer than 200 peer-reviewed publications covering all aspects of environmental, conservation, and policy existed in 2009 (Lake Winnipeg Quota Review Task Force, 2011). Nearly a decade later, a Web of Science search turns up only an additional 160 Lake Winnipeg related publications (2010-2020). By comparison, a search of each of the Laurentian Great Lakes over the 2010-2020 time period returned between 1,680 (Lake Superior) and 2,985 (Lake Ontario) for each lake.

Generally, Lake Winnipeg can be described as a cold, polymictic lake that is subdivided into two distinct basins (commonly referred to as the north and south basins) connected by a narrow channel area (the narrows; Brunkskill et al., 1980). The north and south basins differ in both abiotic and biotic factors; however, the entire lake supports a productive and long-established commercial walleye fishery.

Maximum surface summer temperatures of Lake Winnipeg recorded from July to August averaged between 1999- 2007 were ~19.7˚C in the north basin and ~21.5˚C in the south basin (Environment Canada and Manitoba Water Stewardship, 2011). Predictive models indicate mean mid-summer surface water temperatures will increase between 1.9 and 2.5˚C across the Lake over the next 40 years (Environment Canada and Manitoba Water Stewardship, 2011). The south basin of Lake Winnipeg is approximately 2,789 km^2 with a mean depth of 9.7 m and maximum depth of 14 m (Brunskill et al., 1980). The narrows are approximately 3,450 km^2 with a mean depth of 7.2 m and a maximum depth of 36 m (Brunkskill et al., 1980). Finally, the north basin is approximately 17,520 km^2 with a mean depth of 13.3 m and a maximum depth of 19 m (Brunskill et al., 1980). Due to the shallow nature of the lake and westerly winds, mixing is well established throughout the narrows, south, and north basins. Cases of lake hypoxia and the development of a thermocline are rare, but have been documented in some years in the north basin during late summer (Wassenaar, 2012). Given the maximum depths arcoss both the narrows and north basin, the lake likely can become stratified in maximum depth areas. The south basin is more turbid than that of the north, with respective annual average secchi depths ranging from 0.3-0.76 m in the south basin and 0.66 – 2.13 m across the north basin from 1999-2007 (Environment Canada & Manitoba Water Stewardship, 2011). Lake Winnipeg is situated in an extremely productive agricultral landscape, with a very high watershed to lake ratio of 39:1 (Brunskill et al., 1980). The watershed encompasses four provinces in Canada and four states in the US, totaling approximately 1 000 000 km^2 (Manitoba Water Stewardship, 2011). Due to the broad geographic nature of the watershed across several state, provincial and international boundaries, control and regulation of the landscape has proven challenging in the past (Siddons et al., 2017).

Topographically, the watershed generally has low relief (Brunskill, 1980) and when flooding and heavy rain events occur, rivers reach bankfull rapidly. During flood events, large land areas become inundated with water, leading to soluble phosphorous leaching. This water eventually receeds into the rivers and subsequently, Lake Winnipeg (McCullough et al., 2012). Precipitation within the land covered by the watershed has increased by roughly 10% while runoff due to irrigation and agriculture has almost doubled in the past 50 years (Schindler, et al., 2012). Furthermore, an increase in agriculture thoroughout the watershed has occurred leading to increases in livestock and the use of synthetic fertilizers (Schindler et al., 2012). Specifically, over the past 13 years (1994 – 2007) phosphorus levels in Lake Winnipeg increased by 71% while nitrogen levels increased by only 18% (Armstrong et al., 2011). This increase in nutrient levels over time within the lake (particularly phosphorus) have led to an increase in lake productivity with more frequent algal and cyanobacterial blooms documented in both basins (Environment Canada & Manitoba Water Stewardship, 2011; Schindler et al., 2012). Although the lake has been infrequently monitored over the past 70 years overall, what monitoring has been done indicates that water quality has generally deteriorated (Environment Canada & Manitoba Water Stewardship, 2011; McCullough et al., 2012; Wassenaar & Rao, 2012).

Non-indigenous species found in Lake Winnipeg have contributed to further degredation of overall lake water quality. Common carp (*Cyprinus carpio,* established ~1940s) are well-known disrubters to aquatic ecosystems, proven to reduce aquatic vegetation and heavily increase turbidity in shallow regions, particularly during spawning (Environment Canada & Manitoba Water Stewardship, 2011). Zebra mussels (*Dreissena polymorpha*) were first discovered within the watershed in 2009 and confirmed across the south basin in 2013 (Enders, 2019). Zebra mussels can cause drastic effects on water quality once established across a lake by reducing turbidity and total phosphorus levels (Higgins et al., 2011). The lake has also been invaded by spiny water flea (*Bythotrephes spp*.) which along with zebra mussel have been found to decrease overall growth in walleye (Geisler, 2015; Hansen et al., 2020). Finally rainbow smelt (*Osmerus mordax;* discovered in 1990; Remnant, 1991) can predate on young-of-year (YOY) walleye, reducing walleye biomass (Mercado-silva et al.,2007) while also outcompeting native forage prey species for walleye such as emerald shiner (*Notropis atherinoides*).

The commercial fishery in Lake Winnipeg has always been a gill net fishery (Nicholson, 2007). Historically, mesh sizes were larger and regulatory changes to decrease mesh sizes occurred prior to 1979 (Lysack, 1995). Currently, gill net sizes are set at 76.2 mm in the south basin and narrows throughout the year, and 95.2 mm in the north basin during summer and fall, increasing to 108 mm in the winter (Lake Winnipeg Quota Review Task Force, 2011). Following rainbow smelt invasion, Lake Winnipeg experienced an overall production increase in walleye, linked to both the presence of rainbow smelt and spring flooding events which led to consistently strong walleye year classes (Environment Canada & Manitoba Water Stewardship, 2011). Through 2004 to 2012, roughly 2.5 times the allowable quota of the estimated Maximum Sustainable Yield (MSY) for walleye (1.86 million kgs) was brought in by the commercial fishery, averaging 4.44 million kgs per year (Manitoba Fish and Wildlife, 2009, 2017). However, in recent years, consistent declines in total harvest have been experienced across the lake: 3.2 million kgs 2016/2017, 2.6 million kgs 2017/2018, 2.7 million kgs 2018/2019. Although harvest has declined, it is still above the estimated MSY for walleye throughout Lake Winnipeg. The fishery supports both the local and Indigenous economies, cultural and traditional practices, and plays an essential role in sustaining communities that surround the lake (Environment Canada & Manitoba Water Stewardship, 2011; Probe Reserach Inc, 2018). Population declines in walleye stocks from other commercially fished lakes like Erie (Schneider & Leach, 1977), Black Bay in Lake Superior (Furlong, et al., 2006), Nipigon Bay (Wilson et al., 2007), and Saginaw Bay in Lake Huron (Schneider & Leach, 1977) have demonstrated that walleye are sensitive to intense fishing pressure, and should be closely monitored to ensure sustainable populations.

Walleye

Walleye are found over a wide range of freshwater habitats throughout North America, tolerating a great diversity of environmental parameters (Scott & Crossman, 1998). Walleye are present throughout the province of Manitoba, absent only in the most northern ranges (Watkinson & Stewart, 2004). Maximum growth and production of walleye populations are closely correlated with their ability to occupy both optimal thermal and optical (light) habitat (Chu et al., 2004; Einfalt, et al., 2012; Lester, et al., 2004; Pandit, et al., 2013). The optimal temperature range for walleye is between 18 and 22 ˚C (Hokanson, 1977), while maximum growth has been documented at 21˚C when food availability is unrestricted (Lester et al., 2004). Optimal light intensity for walleye is around a ~2 m secchi depth; generally this occurs at approximately 17% of the depth from the surface to either lake bottom or to the thermocline, if present (Lester et al., 2004).

Walleye possess a *tapetum lucidum* in their retina, allowing them to forage successfully in reduced visibility conditions (Scott & Crossman, 1998). As a result, they are most active during dusk, dawn, night, and may exhibit diurnal behaviour if turbidity levels allow (Scott & Crossman, 1998; Einfalt, et al., 2012). Juvenile walleye begin their lives as planktivores, slowly incorporating small cyprinids and yellow perch (*Perca* *flavescens*) into their diets, until finally transitioning to general piscivores after their first year (Liao et al., 2002; Scott & Crossman, 1998).

Walleye spawn in early spring when the ice breaks and water temperatures reach a minimum of 4˚C (Scott & Crossman, 1998). In Manitoba, this can occur between mid-April to late May (Watkinson & Stewart, 2004). Walleye in Lake Winnipeg either spawn on rocky shoals along the lake shoreline or travel up-river, depositing eggs in rocky substrate (Steward & Watkinson, 2004). Adult walleye in Lake Winnipeg distribute varied diet composition between the north and south basins. South basin walleye diets consist primarily of mayfly larvae (*Ephemeroptera sp*.), emerald shiner, cisco (*Coregonus alpenae*) and yellow perch (Lumb et al., 2012; Sheppard, et al., 2015). North basin walleye diets consisted primarily of rainbow smelt, which made up roughly 85% of their diet year round as well as cisco (Sheppard et al., 2015) despite a broad diversity of available prey in this basin (Lumb et al., 2012). However, rainbow smelt have steadily declined since 2009 across the north basin and are no longer found in trawl surveys (Lumb et al., 2018), suggesting that diets of north basin walleye may have changed as a result.

Prior to the invasion of rainbow smelt, diets of walleye in the north basin of Lake Winnipeg consisted primarily of shiner (*Notropis* sp.) and cisco (Remnant, 1991). Diet shifts in walleye across other lakes invaded by rainbow smelt have also been documented (Lake Huron, Iley & Chaeffer, 2008; Pothoven, et al,. 2016; Lake Erie, Ryan, P.A., 2003; Wisconsin lakes, Mercado-silva, et al., 2007; and smaller Northwestern Ontario lakes, Swanson et al., 2003). Rainbow smelt have a fusiform body shape with no spines and are generally easier for walleye to capture and handle compared to prey with spines. This is suggestive that walleye may shift prey preference and selectively feed on invasive rainbow smelt once established (Scott & Crossman, 1998; Swanson et al., 2003).

Acoustic telemetry and mark-recapture

Over the past 30 years, numerous telemetry studies have been conducted with a dramatic increase in the number of studies completed in the past decade (Crossin et al., 2017; Hussey et al., 2015). Acoustic and biotelemetry technology has been used to gain an improved understanding of both the spatial, physiological, and behavioural ecology on a wide and diverse range of aquatic taxa (Cooke et al., 2004; Hussey et al., 2015; Somero, 2000). The use of telemetry has allowed for the autonomous collection of thousands of data points over a number of years (Cooke et al., 2013; Klimley et al., 1998) revealing previously unknown insights on how aquatic species are interacting and utilizing their environment (Cooke et al., 2004). Understanding how fish are spatially distributed at various times of the year for spawning, rearing, overwintering, and foraging is essential in understanding how a species makes use of their surrounding environment (Cooke et al., 2013). The fine scale data collected from these studies allows for an improved understanding of fish movement ecology and behaviour (Donaldson, et al., 2008) which can subsequently be used to develop well informed management and policy.

To date, most lake-based telemetry studies have used a line or gate array to determine broad scale migration patterns. Gate designs are only able to collect information when a tagged animal leaves or re-enters the gate line (Kraus et al., 2018). Because a tagged animal may pass by the gate but never actually enter the area, these types of detections are difficult to categorize as false or true (Kraus et al., 2018). Likewise, if a tagged individual is only detected a single time on a gate array, it is difficult to determine if emigration or mortality occurred (Kraus et al., 2018). Lake Winnipeg has the benefit of being set up in a 2-dimensional grid array design, allowing for multiple and potentially overlapping detections in some cases. Ultimately, a grid array will permit for a greater understanding of population level dynamics and behavioural movements in known habitat areas (Kraus et al., 2018). Acoustic gate arrays however can still provide managers and scientist with broad scale movement information that may allow them to gain an overview of general fish movement behaviour and patterns. The level of detail and questions being investigated should be reflective across the acoustic array design.

Fish movement data may also be collected by means of mark-recapture studies. Mark recapture studies often take place over long periods of time and have large initial tagging numbers (and frequently low rates of recapture, particularly in large ecosystems like the Great Lakes or Lake Winnipeg; e.g., Ebener et al., 2010). These studies can provide general insight into fish movement ecology, such as long distance migration rates, site fidelity, net mortality, growth rates, and population estimates (Glover, et al., 2008; Lucas & Baras, 2000; Rennie, et al., 2012). Mark-recapture studies allow for a broad-scale interpretation of fish movement over a long period of time. However, mark-recapture data may ultimately fail to provide the full extent of fish movement due to the spatial limits that influence the study (Lucas & Baras, 2000); for example, dead mark-recapture studies often underestimate movement of fishes due to the spatial restrictions of having only a single release and single dead recapture location (Lucas & Baras, 2000). Additionally, studies may be heavily dependent on recapture by commercial fisheries, although recreational and scientific recapture can further contribute to distributional information. A particular concern of the dependency of recapture by commercial fisheries is the introduction of spatial bias as tag recoveries are heavily dependent on where effort is placed (Hilborn, 1990) as well as the exclusion of areas of a lake that are closed permanently or partially to fishing, or not easily accessed by commercial fishers.

Historically, mark-recapture studies were widely used as they are relatively cost effective and were previously one of the only available technologies to study broad scale fish movement. These studies are important as they allow us to understand how species were moving and utilizing a lake historically, assuming they are interpreted with caution and knowledge of the potential for bias. With the development of current acoustic telemetry technology, biologists are now able to conduct studies that allow for a more comprehensive picture of the broad scale movements and fine scale behavioural patterns of fishes.

Previous research

Walleye have been the subject of many telemetry-based studies, due to both their economic importance and position as a native top predator in North American lakes. Walleye in the Laurentian Great Lakes have been subjected to extensive acoustic telemetry studies that have proven successful in revealing previously unknown movement patterns at both broad and fine scales. Long distance movement of walleye has been documented in Lake Huron, where 8% of tagged walleye travelled over 10 km per day within a single month (Hayden et al., 2014). In 2017, Hayden et al. demonstrated that walleye in Lake Huron were more likely to return to spawning areas compared to that of walleye from Lake Erie. The study concluded that due to the lack of readily available spawning habitat in Lake Huron versus Lake Erie, fish were more likely to return to the same spawning areas year after year (Hayden et al., 2017). Walleye spawning site fidelity has been largely accepted as natally-imprinted (Colby & Nepszy, 1980; Spangler, 1977), through investigations using current acoustic telemetry technology paired with genetic analysis have improved our understanding of walleye spawning patterns and behaviour. Telemetry studies that have taken place across Lake Huron (Hayden et al., 2014), Erie (Peat et al., 2015; Raby et al., 2018) and Black Bay, Lake Superior (Mckee, 2018) have revealed populations of walleye that display both migratory and resident behaviours. Further investigation into these two distinct patterns of behaviour have demonstrated that larger walleye in Lake Ontario likely migrate in pursuit of prey species (Hoyle et al., 2017). Across Black Bay in Lake Superior, migrants were observed to achieve a greater overall maximum body size compared with their resident counterparts, likely encountering some benefit related to increased growth (i.e., increased prey availability or energetic status) over residents (Mckee, 2018). Migrant and resident behaviour across Lake Erie has been hypothesized to be in response to water temperature gradients that exist across the lake and forage prey availability (Peat et al., 2015; Raby et al., 2018).

To date, movement and population studies on walleye in Lake Winnipeg have been considered at the genetic and morphological level only. Backhouse et al. (2012) revealed there is little to no genetic variation temporally or spatially at 10 of 12 spawning sites, indicating mixing likely occurs throughout the lake. Stocking programs located in the north and south basin were thought to be responsible for the only two significantly different sites (Riverton and Grand Rapids; Backhouse-James & Docker, 2012). Further to this, a genomic study determined a south to north drift in genetic material was present across the lake, indicating fish from the south basin likely move into and spawn with north basin fish (Thorstensen et al., 2020). A morphological study that analyzed scale wavelet shape between basins found significant differences between south and north sampling locations, indicating ecological speciation likely exists between basins (Watkinson & Gillis, 2005). Some walleye within Lake Winnipeg also exhibit phenotypic colouration differences, referred to as “greenbacks” (Stewart and Watkinson, 2004). Walleye in the north basin have been documented as having slower growth and delayed age-at-maturity, with longer life spans compared to that of walleye captured in the south basin fish (Johnston et al., 2012). Additionally, a dwarf morphotype of walleye is present, found only across the south basin (Moles et al,. 2010; Sheppard et al., 2018). Generally, the lake is managed as stock-specific populations within each respective basin (different mesh net size regulations) as movement behaviour in the lake is still not well understood. Due to the contrasting conclusions of previous studies regarding the differences between walleye found in the north and south basins of Lake Winnipeg (e.g., genetic studies indicating no differences between basins, morphological studies suggesting differences between basins), the analysis of data from current telemetry studies and past mark-recapture studies of walleye should lead to greater insight into patterns of movement between and within each basin.

1.2 Objectives and hypotheses

This thesis work will use both historical mark-recapture data from the 1970s along with current acoustic telemetry data to assess movement and survival rates of walleye over time. I focus on two separate objectives to determine movement and survival rates over the course of both contemporary and historical studies, and describe south basin spawning walleye movement across seasons, investigating the potential for resident and migratory behaviours in this population. My objectives were:

1. To determine walleye survival and movement rates for contemporary and historical datasets across north and south basins, considering the influence of body size at the time of tagging and its influence on movement across the lake. This objective was accomplished using Cormack-Jolly-Seber models (specifically, multi-state live-dead modelling) using the mark-recapture software, program MARK.

2. Having established resident and migrant behavioural types in walleye tagged in the south basin in the contemporary telemetry study, I sought to evaluate how movement

varied on a seasonal basis. I determined the home (95%) and core (50%) space use of these two behavioural types using kernel density estimators to assess differences in seasonal space use between groups. Furthermore, this objective also assessed differences in latitudinal distribution using centroid locations from kernel density estimators and associated home and core range polygons.

Changes in water quality (eutrophication), fishing pressure, invasive species establishment, and general morphological differences across basins may have influenced and shaped patterns of fish movement behaviour over the past 50 years. Furthermore, relatively recent studies across the Great Lakes have revealed long distances migration across various walleye populations. Therefore, I hypothesized that movement between basins has likely has been occurring over the small temporal time scale of 50 years investigated here, given the recent genetic and genomic studies that suggest mixing between north and south basin walleye (Backhouse-James & Docker, 2012; Thorstensen et al., 2020), and work conducted across the Great Lakes which has effectively demonstrated long distance migration across walleye in large lake systems is a relatively common behaviour. However, rates at which walleye use either basins may have changed to reflect a change in overall lake condition and habitat. Furthermore, I hypothesized larger individuals would be more likely to move given that they are better able to account for the metabolic energetic costs associated with long distance travel (Roff, 1988).

1.3 Significance

The overall lack of knowledge for walleye movement ecology in Lake Winnipeg and differing conclusions as to whether separate populations occupy the lake provides a unique case study in the importance of understanding fish movement patterns to understand the biology of the system under investigation. Information on fish movement rates is essential in order to properly manage and regulate such a heavily fished lake (both commercially and recreationally). This work will be important to provide answers to these questions and is the first formal investigation we know of to use mark-recapture and bioacoustics to attain movement and survival rates of walleye in Lake Winnipeg. If movement and survival rates have changed dramatically over time, this analysis may help to identify what ecological changes have occurred that might influence walleye behaviour. Information gathered from this research is hoped to aid policy and fisheries managers when developing new regulations for both the commercial and recreational fishery. Finally, this work may also act as a baseline for any future movement studies on walleye in Lake Winnipeg.

Chapter 2. Historical and contemporary movement and survival rates of walleye (*Sander vitreus)* in Lake Winnipeg, Canada

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Disclaimer

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Author contributions to the submitted manuscript version presented here are as follows: DW, EE, GK, NT and MR conceived the study; DW, EE, GK, NT and MR secured funding for the study; DW, NT, EE, and CC conducted field work; GK, DW and CC provided data; NT, CC and MR conducted data analysis; NT prepared figures; NT and MR wrote the manuscript, and all authors participated in the editing of the manuscript for final submission.

2.1 Abstract

Understanding patterns of fish movement across large lake ecosystems is essential for determining appropriate management practices as differences in movement behaviour can influence life history traits such as growth and survival. Lake Winnipeg in Manitoba, Canada supports the 2nd largest walleye (*Sander vitreus*) commercial fishery in North America, however very little is known regarding inter-basin movement across the lake. Here, we used mark-recapture studies to estimate movement and survival of walleye between basins of Lake Winnipeg in historical and contemporary contexts. This comparison was facilitated using a tag-recovery study competed during 1976–1979 and a contemporary (2017–2019) acoustic telemetry study. Mark-recapture models revealed comparably low annual transitions between basins from both historical (0.3–1.2%) and contemporary datasets (7–8.5%). Historically, fish >300 mm more frequently moved in a south to north direction. Contemporary estimates suggest similar size-based directionality in that fish >350 mm were always more likely to move in a south-north direction, while fish moving north to south were increasingly more likely to with increasing body size. We also observed variation in seasonal movement and survival between basins across the contemporary dataset, with the greatest movement in both directions occurring during the fall. Contemporary annual survival derived from mark-recapture models was 37%, while annual historic survival was estimated at 54%. Our finding of relatively consistent patterns of low but significant movement along with influences of body size and its impact on both movement and survival across basins in Lake Winnipeg spanning over 50 years will provide relevant insight into fisheries management and policy across the lake

Keywords: acoustic telemetry; mark-recapture; Cormack-Jolly-Seber model; fish movement

2.2 Introduction

Quantifying movement patterns and behaviour can reveal seasonal variation in patterns of habitat use (Van Moorter et al., 2016). A clear understanding of species movement patterns is of even greater relevance when the species of interest provides ecosystem services, such as a fishery. Migration, and movement generally, is inherently energetically costly (Roff, 1988) and is often driven by resource acquisition (Jonsson and Jonsson, 2006; Rennie et al., 2012a; Rennie et al., 2012b). As such, movement is intimately linked to life history traits such as growth and survival (Rennie et al., 2012a; Roff, 1988). As freshwater systems undergo fluctuations and alterations due to anthropogenic, natural, and climate related changes, these impacts may affect fish and their subsequent movement and survival patterns (Allan et al., 2005; Nathan et al., 2008; Richter et al., 1997).

Freshwater fish migration is a relatively common phenomenon and often associated with exploiting differences in habitats to gain a fitness advantage (Gross et al., 1988). Both resident and migratory individuals are regularly observed in the same population, suggesting some energetic threshold may be required to initiate movement (or criteria for individuals to evaluate the benefits of movement vs. staying) may be involved (Bronmark et al., 2013; Chapman et al., 2011; Lucas and Baras, 2000). Habitat heterogeneity is a particular feature of large lake ecosystems (Eadie and Keast, 1984), and has been implicated in long-range migrations for several Great Lakes species (Ebener et al., 2010; Wang et al., 2007). Recent walleye (*Sander vitreus*) movement studies on the Laurentian Great Lakes have revealed significant long distance migration patterns in populations (Hayden et al., 2014; Mckee, 2018) driven by factors including spawning site fidelity (Hayden et al., 2017; Wang et al., 2007) and thermal preference (Peat et al., 2015). Differences in movement strategies within a population have also been shown to be associated with different growth rates (Mckee, 2018) suggesting the decision to migrate can have a significant impact on the life history of fish (growth and survival) in freshwater systems. Thus, a clearer understanding of the factors associated with fish movement can aid in the development of better management strategies and conservation efforts (Brooks et al., 2017; Crossin et al., 2017; Donaldson et al., 2014). This is true both in terms of understanding how migrating stocks across regions may respond to regional differences in commercial and recreational fishing regulations (Crossin et al., 2017) but also in recognizing potential growth differences among sub-populations in estimating commonly growth-derived estimates of life history traits such as survival, mortality, size, and age at maturity (Charnov et al., 1993; Ricker, 1975)

Lake Winnipeg is the 11th largest lake in the world and supports one of the largest walleye fisheries in North America, second only to Lake Erie (Franzin et al., 2003). Walleye play a significant role in the Lake Winnipeg ecosystem as a native top predator species while also contributing millions of dollars in revenue to the Province of

Manitoba annually through commercial and recreational fishing activity (Probe Reserach Inc, 2018). Despite their relative importance in both the ecosystem and the regional economy, very little is understood regarding their movement and survival across the lake. Past evidence regarding differentiation between north and south basin walleye as distinct stocks is conflicting. A genetic analysis concluded there is no evidence to support separate walleye population structures between the basins (Backhouse-James and Docker, 2012). However, a recent RNA study reported weak population structure across north and south basins presenting evidence of a low rate of mixing between basins (Thorstensen et al., 2020). By contrast, significant differences between walleye from the north and south basins have been reported in growth rate, body condition, diet, and scale morphology (Johnston et al., 2012; Moles et al., 2010; Sheppard et al., 2015, 2018; Watkinson and Gillis, 2005) suggesting the potential for ecological specialization between basins. Uncertainty remains as to the degree walleye use the entire lake over the course of a given year versus remaining within each of the basins.

To evaluate and compare historical and contemporary movement and survival rates between the north and south basins of Lake Winnipeg, we applied a multi-state live-dead mark-recapture model (Brownie et al., 1993; Kendall et al., 2006; Lebreton et al., 2009; Schwarz et al., 1993; White et al., 2006)to fish tagging (historical) and acoustic telemetry (contemporary) data across the lake. Where possible, we investigated movement and survival on a seasonal basis, as walleye movement has been documented elsewhere to vary seasonally (Hayden et al., 2017, 2014). In addition, we evaluated the role of fish size on inter-basin movement rates. Based on findings from genetic studies (Backhouse-James and Docker, 2012; Thorstensen et al., 2020), we hypothesised that movement between the two basins occurs but is limited. We expected differences in movement and survival between the time periods given the increased effort in harvest, and changes in limnological conditions (Nicholson, 2007; Schindler et al., 2012). Finally, we tested if larger fish demonstrate greater rates of inter-basin movement, as they are better suited to manage the increased bioenergetic costs associated with moving larger distances (Roff, 1988).

2.3 Methods

Study area

Lake Winnipeg is located within the Province of Manitoba, Canada and is the third largest freshwater lake entirely within Canadian borders (Johnston et al., 2012). The lake can be divided into two relatively separate basins, one in the north and one in the south (Fig. 2.1). The north and south basins are connected by a narrow channel area which for the purposes of this study is not considered as a distinct and separate region of the lake (see below). The south and north basin differ from one another in both their biotic and abiotic features. The south basin is approximately 2,900 km^2 with a mean depth of 9.7 m and Secchi depths of 10– 100 cm. By contrast, the north basin is larger, deeper, and clearer than the south basin (approximately 19,000 km^2, mean depth of 13.3 m, and Secchi depths between 50–260 cm (Brunskill et al., 1980; Wassenaar et al., 2012). Doghead Point (51.745428, -96.826436) is located relatively central within the channel, and was used in this study as the dividing feature between the south and north basins due to its relatively high receiver coverage for the area covered (Fig. 2.1).

Therefore, Doghead Point and all receiver gates south were considered within the south basin, whereas all gates north of Doghead Point were considered the north basin.

Historical movement study

Walleye were tagged during the first two of three years over the course of the historical study (Table 2.1). In 1974, tagging took place from May 29th to August 30th and from May 6th to October 30th in 1975 (Table 2.1). Over both years of tagging, a total of 7,991 walleye were captured and released into Lake Winnipeg at various locations across the basins (Fig. 2.1). Approximately 10% of the tagged fish were recaptured between June 6th, 1974 and May 29th, 1977 (Table 2.1). Average fork length at tagging for walleye across the north basin was 385 mm and 382 mm throughout the south basin (range: 210–660 mm). Of all fish tagged, 87 fish had no associated fork length recorded at tagging. Historical tag returns were exclusively from commercial fishers operating on the lake. Fishers were paid $1.00 CDN for each tag returned; the equivalent of $4.78 CDN in 2020. Historical reporting rates for the commercial fishery on Lake Winnipeg are unknown but estimates determined on Lake Erie ranged from 10–17% annually (Vandergoot et al., 2012). Fish were originally captured and tagged using a combination of short set gill netting, trap, and seine netting methods. Fish were tagged with individually numbered external anchor tags (Floy® T-Bar Anchor Tag, FD-94, 25 mm monofilament; Floy Tag Inc., Seattle, WA, USA) inserted around the first and second dorsal fins between the pterygiophores. A spatial overlay grid measuring 8.5 by 8.5 km^2 (Appendix A Fig. A1) was used to assign initial tagging and subsequent recapture locations.

Contemporary movement study

In 2016, a study was initiated by Fisheries and Oceans Canada to monitor fish movement in the Lake Winnipeg basin. Receivers were placed throughout the lake in a grid style array during the 2016 and 2017 field seasons, deployed receivers covered the entirety of the south basin up to the middle of the north basin (Kraus et al., 2018; Fig B2). To address broad-scale movement patterns at a similarly coarse scale of resolution as the historical survey, a subset of receivers was selected to form gates across the lake. During the 2016 field season, prior to any walleye tagging activity 17 receivers (VR2W, VR2Tx, 69 kHz; Vemco, Innovasea, Bedford, NS, Canada; Fig. 2.1) were deployed throughout Lake Winnipeg covering the south basin from the Red River to Doghead Point. Three of these receivers were deployed at Doghead Point, spaced 1.5km and 0.5km across the 2 km channel. This ensured a ~80% and ~96% detection probability between the receivers. During 2018, the middle receiver across the channel was lost leaving roughly a 2 km spacing between the two remaining receivers (~70% detection probability; Chapter 3, Fig. 3.6). During the spring of 2017, 12 receivers (VR2W, VR2Tx, 69 kHz; Vemco, Innovasea, Bedford, NS, Canada; Fig. 2.1) were deployed across the north basin. A detailed description of receiver and gate spacing is located in Appendix B.

During the spring and fall of 2017, walleye were tagged with acoustic transmitters (V16-4H, Vemco) in the south and north basins (Table 2.2; Fig. 2.1) with average fork length at tagging 597 mm in the south basin and 543 mm in the north basin (range: 452–721 mm). During the spring of 2018, an additional tagging effort took place in the south and north basins using a combination of tag sizes to incorporate smaller bodied individuals (V13, Vemco; Table 2.2; Fig. 2.1). Average fork length of tagged walleye during 2018 was 482 mm in the south and 448 mm in the north basin (range: 344–735 mm). Acoustic transmitter tags had a nominal random delay range of 85-165 s to ensure equal probabilities at each random delay and to also reduce the probability of transmitter collisions on receivers. Walleye tagged in 2017 and 2018 were captured using an electrofishing boat (Smith-Root SR20-EH; GPP 5.0; 100-500 V). Prior to surgery, fish were placed in holding tanks filled with aerated ambient lake water. Fish were immobilized using a Portable Electroanethesia System (PES, Smith-Root, 100 HZ, 25% duty cycle, 40 V for ~5 s, Vancouver, WA, USA; Vandergoot et al., 2011). Fish were then placed in a padded trough while respiration was maintained through constant irrigation over the gills. A 3 cm incision was made midventral on the abdomen and the tag was inserted within the body cavity of the fish. Incisions were closed with 2–3 interrupted sutures (standard surgical knots; 3-0 polydioxanone-II violet monofilament; Ethicon, Cincinnati, OH, USA). Fish also received an external floy tag (Floy T-bar anchor; Floy Tag Inc.) inserted into the muscle between the pterygiophores below the base of the second dorsal fin. Floy tags contained a unique identification number along with a telephone number for reporting purposes. Fish were placed into recovery holding tanks and released when they regained the ability to physically swim away from a releaser's hand. Walleye were sexed following the ventral surgical incision via visual inspection prior to the insertion of the acoustic telemetry tag. Physical recaptures of fish were reported through both the commercial and recreational fishery. Fish handling, capture, and surgery were approved by Canadian Council on Animal Use Protocols administered by

Lakehead University (Project ID: 1466383) and Fisheries and Oceans Canada (FWI-ACC-2017-001; FWI-ACC-2018-001).

Multi-state live-dead modelling

A multi-state live-dead mark-recapture analysis (Lebreton et al., 2009; White et al., 2007) was chosen to evaluate fish movement and survivorship to account for both live (detections encountered through telemetry equipment) and dead (commercial and recreational recaptures) reports. Multi-state live-dead models allow for the estimation of four parameters: survival (ϕ), movement (ψ), resight (p), and reporting rate (r). Detailed assumptions of the model can be found in Appendix C. Our main interest in using this model was to determine estimates of survival (ϕ) and movement (ψ) across the basins. Additional parameter estimates resight (p) and reporting rate (r) were used in model fitting but were not the focus of the current and historical studies and are not reported on further here. Additionally, historical survival estimates derived from the model were surprisingly low and as a result are not reported here (potentially a result of low sample size, low recapture rate, and no live resight information). We opted to independently calculate historical survival from tag and recapture data incorporating estimated rates of tag loss, reported captures, and natural mortality reported elsewhere. For multi-state mark-recapture models, we considered two different basins for this analysis as states (south and north). Mark-recapture live-dead models were run using program MARK (White et al., 1999; White et al., 2006) via Rmark (Laake et al., 2019) in the R statistical programming environment (R Core Team, 2019).

Data preparation

The historical mark-recapture study took place between May 30th, 1974 to March 31st, 1977 and included 148 weekly time steps (approx. 3 years) while the contemporary telemetry study took place from May 5th, 2017 until April 17th, 2019 with 103 weekly time steps (approx. 2 years). We used weekly time steps to provide a detailed temporal resolution and fit seasonal and annual groupings to balance overparameterization while implementing biologically relevant time bins. Weekly encounter histories for individual fish and fork length (mm) in both datasets were developed using program R (R Core Team, 2019).

Telemetry data was filtered for false detections using the R package GLATOS (Binder et al., 2018); false detections occur when multiple transmissions collide at a receiver station and need to be subsequently removed from the dataset (Pincock, 2012). Additionally, individual fish abacus plots using all deployed receivers across the lake (Appendix D, Fig D1) were visually assessed to evaluate tag failure. We removed one individual in 2017 and 10 individuals in 2018 tagged at Sandy Bar (south basin) which had zero detections recorded, indicating likely tag failure. The fate of individuals (i.e., probable deaths) were also assessed using the full array grid. Individuals that were frequently detected on multiple receivers on the array south of Doghead Point and then suddenly no longer detected for the duration of the study were assumed to have been removed (i.e., harvested), or died away from a receiver and assigned dead at the time and place of the last subsequent detection. Given the extensive array in the south basin (Fig. B2), the probability of being alive and unsighted on any receiver in this basin were deemed to be extremely low. Similarly, walleye that were subsequently detected multiple times on the same receiver for more than two weeks (excluding winter months when fish were observed to be more lethargic) were assessed as dead or having dropped a tag. In both cases, we noted the first-time bin this occurred and the location and added this information to the encounter history file (e.g., as ‘known’ dead). Fish that went undetected north of Doghead Point and were not observed again were assumed to be at liberty but not detected due to the lack of receiver coverage across the north basin, as it was not possible to determine at what point in time they may have been removed from the study, if at all.

We opted to group the weekly encounter history data into seasonal time bins to address questions of inter-basin movement and survival differences on a seasonal basis across a given year in the contemporary dataset. Seasonal time bins varied slightly during the spring in the contemporary dataset due to both the restrictions associated with the timing of tagging and receiver downloads. Seasons were determined using ice-on and ice-off events, ambient air temperatures, and knowledge of relative walleye spring spawn and fall run events to encapsulate biologically meaningful events. We chose a longer time bin for winter consisting of 24 weeks to capture short but active fall and spring seasons. During initial data investigation, individual walleye were seen overwintering close to known spawning locations indicating pre-spawn movement activity was significantly less than that of post-spawn activity. Based on these patterns, the spring grouping incorporated behaviours associated with spawn and post spawn movement off the spawning grounds. As walleye are known to have increased periods of movement during spring and fall, well documented in other movement studies (Hayden et al., 2017; Kirby et al., 2017; Mckee, 2018; Peat et al., 2015; Wang et al., 2007), we included models with interaction terms between season and basin to capture both inter-basin movement and its potential to vary seasonally. Based on these considerations, spring consisted of seven weekly bins in 2017 (May 5th–June 18th), and eight for spring 2018 (April 24–June 18th). In both 2017 and 2018, summer consisted of 12 weekly bins (June 19th–September 10th), fall consisted of eight weekly time bins (September 11th– November 5th), and winter consisted of 24 weekly time bins (November 6th–April 23rd).

Historical data was grouped on a yearly basis. Given the lack of detail across the historical dataset (only release and recapture data at most for each individual) and to avoid overparameterization, models were constrained to assess the data on an annual basis only; May 30th, 1974 to May 22nd, 1975 (52 weekly time bins), May 29th, 1975 – May 20th, 1976 (52 weekly time bins), May 27th, 1976 – March 31st, 1977 (45 weekly time bins). To allow for more direct comparisons between historical and contemporary datasets, we also considered yearly time bins for the contemporary telemetry data (ignoring seasons). Weekly telemetry data in the contemporary dataset was binned by year from May 5th, 2017 to April 24th, 2018 (53 weekly time bins) and from May 1st, 2018 to May 7th, 2019 (54 weekly time bins). Historically, fish were assigned a basin location based on initial tag and final recapture locations determined through a reported location on the grid layout (Appendix A, Fig. A1). For contemporary telemetry data, fish were assigned a basin location of either south or north. This location was determined based off the weighted average of detections across the gates within a given week (either seasonally or annually). Weekly basin locations were defined as the individual weighted average of detections across the gates, assigning a basin location of south, north, or no location if not detected. Historical encounter history files for analysis with fork length (mm) and without, as well as the contemporary encounter history files for the seasonal and annual comparison analysis with associated fork lengths (mm) were developed.

We evaluated a pre-defined set of models that were tested against the most general model. We determined three sub models of interest for movement and survival and two sub models for resight and reporting rate parameters for a total of 36 possible parameter combinations across historical and contemporary datasets (Appendix E, Table E1; Table E2). Top models from pre-defined model parameters were evaluated for model fit, with the top models with the lowest AIC values reported for historical and contemporary datasets, compared using ΔAICc (Table 2.3; Table 2.4). Using the top model fits for both the historical and contemporary data, we additionally evaluated the added explanatory effect of fork length at tagging (as a fork length by basin interaction term in the model) as a continuous covariate on movement. Additionally, because weekly time bins were used to originally bin data in the encounter histories files, model estimates of survival and movement were estimated on a weekly basis across a given season.

To determine survival and movement on an annual time scale, we adjusted the weekly estimates from the models to represent annual estimates of movement and annual survival. Furthermore, to compare the historical and contemporary datasets and their estimated parameter values using a similar model parameterization, we fit the historical top model structure (excluding the body size covariate) to the contemporary acoustic telemetry dataset.

Adjusted movement and independent survival estimates

Annual historical movement estimates were adjusted to account for tag loss, as the model used to evaluate movement assumes 100% tag retention (White et al., 2006). The number of fish remaining in the lake each year after tag shedding (N') was estimated as the number of fish tagged in each year (N; Table 2.1) adjusted for annual tag loss at 21.9% (SD=0.02; $\hat{\tau}$; 0.781; Koenigs et al., 2013) and individuals reported captured (n; Table 2.1; Eq. 1). We then calculated the number of tagged fish that did not move across the basin (f) as ($N' - \psi * N$), where ψ is the movement estimate derived from mark-recapture models (Eq. 2). We then used Eq. 3 to determine the percent of fish that remained in each basin (%*res*). This then allowed us to use Eq. 4 to determine the adjusted annual movement estimate $(\hat{\psi})$ accounting for tag losses. Both unadjusted and adjusted historical movement estimates are reported (Table 2.5).

$$N' = (N * \hat{\tau}) - \mathrm{n} \qquad \text{Eq. 1}$$

$$f = N' - (\psi * N) \qquad \text{Eq. 2}$$

$$\%res = f/N' \qquad \text{Eq. 3}$$

$$\hat{\psi} = 100\% - \%res \qquad \text{Eq. 4}$$

Given the design of the historical study (e.g., no observations of live resights), the model was poorly suited for estimating survival. We therefore opted to independently calculate survival while accounting for tag loss, natural mortality, and reported captures across the study. We considered accounting for commercial reporting rate using an estimate derived from a Lake Erie walleye study (10–15%; Vandergoot et al., 2012), however, this produced unrealistically small estimates of survival (7–9%) and were not considered further. We used equation 5 to determine the number of individuals that retained their tags (N_{TL}) in a given year where $\hat{\tau}$ is annual tag retention (0.781; Koenigs et al., 2013). We additionally removed the reported individuals each year (*n*) from total individuals remaining after tag loss to determine the number of fish at liberty (ω ; Eq. 6; Table 2.5). We then applied annual instantaneous natural mortality (*M*) at 33% (Vetter, 1987; Eq. 7). Total survival was then estimated as the number of fish remaining in each year (Eq. 8).

$$N_{TL} = N * \hat{\tau} \qquad \text{Eq. 5}$$

$$\omega = N_{TL} - n \qquad \text{Eq. 6}$$

$$N' = \omega * (1 - M) \qquad \text{Eq. 7}$$

$$\hat{\phi} = N'/N_{TL} \qquad \text{Eq. 8}$$

2.4 Results

Historical Movement

Movement probability estimates for the historical survey varied among years or by basin with none of the top models including a basin by time interaction. The top model indicated movement varied by basin and was not time dependent (Table 2.3). South to north basin movement on an annual basis was estimated at 1.1% (β= -4.48 SE= 0.212) while north to south movement was estimated at 0.35% (β= -1.14 SE= 0.243) across the duration of the study. The second top model (ΔAICc 2.15) indicated annual differences in movement probabilities. After adjustments were made for tag losses, these estimates increased slightly; annual corrected movement estimates increased to 0.3% in year 1, 1.2% in year 2, and 0.4% in year 3 (Table 2.5). The inclusion of fork length at capture as a stratum covariate was incorporated into the top model and resulted in an overall better model fit (ΔAICc -99.75). The effect of body size at tagging positively affected movement in a south to north direction (β_{FL}=0.005 SE= 0.002) and was slightly negative in a north to south direction (β_{FL}=-0.014 SE=0.003). Historically, larger fish (>300 mm) in the south basin were more likely to move to the north basin, whereas only small individuals (<300 mm) although a very minimal effect were more likely to move into the south basin from the north (Fig. 2.2).

Historical Survival

Parameterization of survival probability estimates for the historical tagging study varied between the top four models (Table 2.3); estimates were either constant across both basins and over the course of the study or varied on an annual basis. However, estimates of survival from the multi-state live dead model were unreasonably low (~8%) and were not considered further (see methods). Independent survival estimates, which accounted for tag loss, natural mortality, and reported captures (see methods) were

54% on average across all three years (Table 2.5), which were closer to contemporary estimates.

Contemporary Movement

Movement models in the contemporary dataset were tested for both basin (north and south) by time (season) interactions and additive effects (Table 2.4). Top model only considered based on greatest weight of evidence from AIC (Table 2.4). Inter-basin movement probabilities from the south to north basin were consistently higher than in a north to south direction (Fig. 2.3). Inter-basin movement between basins tended to be lowest in winter and summer and highest in fall and spring (Fig. 2.3). As with the historical data, the inclusion of fork length at tagging as a covariate improved model fit (ΔAICc -22.8), but in an opposing pattern. Unlike historical estimates, a small negative effect of fork length on inter-basin movement from the south to north basin was noted (β_{FL} = -0.0004 SE = 0.0006), while a positive effect of fork length on inter-basin movement from the north to south basin was observed (β_{FL} = 0.005 SE = 0.0008; Fig. 2.2). However, inter-basin movement was consistently higher from the south to north across all sizes of tagged fish, being equivalent only at the largest body sizes (Fig. 2.2). Thus, smaller fish in the south basin were slightly more likely to move to the north basin than larger fish, whereas only the largest individuals were as likely to move in either direction.

Contemporary Survival

Survival models were fit with either a basin by time interaction or with additive effects (Table 2.4). Survival estimates among the top two models included a basin by season interaction (Fig. 2.3). Fall survival in both years tended to be higher in the south basin compared to the north basin. While winter survival was greater in the north basin in 2017, this was not observed in 2018. In both basins, survival appeared to increase from spring to winter, declining again from winter to spring (Fig. 2.3).

Comparison of historical and contemporary models

The historical top model structure included constant survival across basins and inter-basin movement rates, with no temporal effects of season or time. Survival estimates derived from the mark-recapture models were unreasonably low therefore we used the independent calculations of survival to compare to the current survival estimates. Independent annual historical estimates of survival were estimated at 47% during the first year, 66% during the second, and 51% during the third year of the study. After adjusting the model estimates of weekly survival to a standardized annual survival estimate, contemporary annual survival was estimated at 37% (β = -2.58 SE = 0.056) across the duration of the study; 44.9% (β = -0.20 SE = 0.127) during the first year, and 26.8% (β = -0.798 SE = 0.204) during the second year (Table 2.4). Annual movement transition probability across the lake (with no directionality considered) for the contemporary dataset was 7% (β = -2.57 SE = 0.055) during 2017 and 8.6% (β = 0.22 SE = 0.083) in 2018, compared to yearly annual historical estimates of <1% (Table 2.5). However, after adjusting yearly historical movement to account for tag loss, historical movement transition probability ranged from 0.3–1.2% annually (Table 2.5).

2.5 Discussion

In both the historical and contemporary data, our models revealed a small but measurable proportion of tagged walleye moving between basins in both north and southward directions, with movement primarily from the south to north basin. This consistency in inter-basin movement between studies was observed despite differences in the study design and five decades separating the two studies. This consistent pattern of greater movement from the south to north basin may be due to several reasons. First, this direction of movement (south to north) matches the movement of water flow in the basin, as Lake Winnipeg empties in the north into the Nelson River and eventually into Hudson Bay. Second, potentially higher walleye production in the south basin may result in northward movement as an ‘overflow’ effect to relieve carrying capacity in the south basin; previous studies have shown that walleye biomass (juvenile and smaller bodied fish) tends to be greater in the south basin based on gill net and pelagic trawl surveys (Johnston et al., 2012; Lumb et al., 2018, 2012).

Significantly, our findings support previous molecular studies showing low genetic differentiation between basins (Backhouse-James and Docker, 2012) and recent work showing gene flow primarily occurring between basins in a south to north direction (Thorstensen et al., 2020), and strongly suggest that these patterns are a consequence of walleye movement in the lake. While these molecular studies were suggestive of movement between basins to support genetic results, the current study provides the first direct evidence for movements that would support gene flow, and further, demonstrates primarily south to north movement patterns that are consistent with recently reported patterns of south to north transmission of genetic material (Thorstensen et al., 2020). As such, this sum of evidence suggests that morphometric differences previously documented between north and south basin walleye (Johnston et al., 2012; Sheppard et al., 2018; Watkinson et al., 2004) are likely due to phenotypic plasticity, rather than any genetically-based population divergence.

Consistent inter-basin movement patterns across both historical and contemporary studies from the south to north basin may also reflect variation among basins with regards to historical and current patterns of prey availability. Fish moving north may be doing so as a response to the reduce mortality associated with commercial and recreational fishing pressures in the south basin which is greater and more concentrated. Lake Winnipeg has supported an active gill net fishery since the early 1890s, which has removed tens of millions of kilograms of walleye from the lake through both commercial and recreational activities (Environment Canada and Manitoba Water Stewardship, 2011; Heuring, 1993). Individuals who have adopted a strategy where they move north at a fast rate during the spring may benefit from an increase in survival over the years as they in turn reduce their vulnerability to selection by commercial and recreational gear in this area. However, a lack of prey availability in the north basin due to the recent collapse of rainbow smelt (*Osmerus mordax*) around 2012 (Lumb et al., 2018) may have resulted in northward-migrating fish pursuing a favourable prey that is no longer available in high densities (Lumb et al., 2018; Sheppard et al., 2015). Thus, any potential survival differential that once may have existed from avoidance from south basin fisheries may now be eliminated due to the currently reduced prey availability in the north basin.

Though fish in both the historical and contemporary study were more likely to move from the south to the north basin, the effect of fish size on inter-basin movement probabilities differed slightly. Historically, fish >300 mm were increasingly more likely to move from the south to north basin. This is likely also a reflection of basin-specific differences in commercial fishing pressure, where the north basin applies larger mesh sizes in gill nets (95 mm in summer and fall, 108 mm in winter) than in the south basin (762 mm year round; Lake Winnipeg Quota Review Task Force, 2011). Considering all historical individuals were recaptured via the commercial fishery, bias associated with gill net mesh size is likely very strong and results gathered here should be interpreted so. Currently, smaller walleye were only marginally more likely than larger bodied individuals to move from the south to north basin, whereas the probability of movement of fish from the north to south basin increased greatly with fish size. Differences in methodology between historical and contemporary time periods resulted in differences in the mean size of fish tagged, and we were unable to evaluate movement of fish <300 mm in the contemporary study as was done in the historical dataset. However, extrapolating patterns of contemporary effects of fish size on inter-basin movement towards smaller sizes suggests that the effect of size on inter-basin movement probabilities likely has changed between time periods, primarily indicating that larger walleye are now more likely than smaller fish to move from the north to south basin compared to historical patterns. Size-dependent migration has been documented in other movement studies on walleye (Bowlby and Hoyle, 2011; Mckee, 2018; Wang et al., 2007); larger fish tend to migrate over smaller individuals as they are able to better able to account for the bioenergetic costs associated with travelling long distances (Lucas et al., 2000; Woolnough et al., 2009). However, further analysis would be required to understand if fish currently remain throughout the south basin or move back into the north basin during the fall or any season following which is addressed throughout Chapter 3.

The contemporary data set indicated increased walleye inter-basin movement during fall, with the lowest inter-basin movement occurring in summer and winter (2017) across both basins. The south basin is more shallow, turbid, and does not develop a thermocline across summer months compared with that of the deeper, cooler north basin that can develop a thermocline during the summer, though rare (Brunskill et al., 1980; Stainton, 2005). Additionally, Lake Winnipeg extends just over 4° of latitude, which allows for a north-south gradient of water temperature to exist, as well as delays in ice-on and off events between basins that are roughly two weeks apart (Brunskill et al., 1980; Environment Canada and Manitoba Water Stewardship, 2011). South to north movement in the spring may therefore be in response to individuals moving into cooler water as temperatures in the south basin begin to reach the upper limits of maximum optimal conditions for walleye; similar thermally-dependent movement behaviour has been proposed in both Lake Erie and Lake Huron (Hayden et al., 2014; Raby et al., 2018; Wang et al., 2007). Additionally, the Red River carries the warmest water into Lake Winnipeg which typically allows for individuals to spawn up to a month earlier compared with other known spawning locations across the lake. As such, walleye spawning in the Red River may take advantage of the opportunity to spawn earlier in the year followed by large scale movements into more thermally optimal temperatures across the north basin. This may permit higher growth rates in individuals who take advantage of optimal thermal habitats via migration while also accessing a longer growth period (due to earlier spawning in the Red River).

Across the winter and summer seasons, reductions in inter-basin movement between the basins occurred over both years. This indicates that fish were more likely to make localized movements within each basin during both the winter and summer seasons. Similar behaviour was noted across Black Bay in Lake Superior where tagged walleye were observed to remain localized to a single area of the bay across the winter months but were most mobile in the late spring and early fall (Mckee, 2018). Walleye may stage themselves in the winter close to spring spawning grounds, allowing for energy conservation by remaining close to spawning areas while also decreasing inter-basin movement (assuming sufficient prey availability in the region). During the observed summer decline in movement behaviour, walleye may have been constrained by increased energetic costs of travel through supra-optimal warmer water temperatures, making them less likely to undergo inter-basin movement during the summer months.

Contemporary survival rates appear to vary between basins dependent on season. Survival in the north basin was lower than in the south basin during the fall across both years, but higher than the south basin in winter 2017 (though not in 2018), while summer between the basins was similar in 2018 with the north slightly higher than the south in 2017. In both basins, winter survival appeared to be higher than in the spring and summer seasons. Changes in relative survival between the two basins may in part be due to differences in the timing of commercial fishing activities where the fall season opens lake wide on September 1st and the spring season opens 1-2 weeks earlier in the south. Individuals across the north basin during the fall may be at an increased risk of capture due to inter-basin movement in response to cooling water temperatures which occur earlier in the north. The opening of the fishery across the south basin during the spring subject's walleye to a longer duration of risk via capture given the earlier opening and longer season. Additionally, differences in gill net mesh sizes would reflect differences in survival across different sized individuals increasing vulnerability in some individuals. Finally, the acoustic telemetry study tagged a greater number of individuals across the south basin particularly during the first year of tagging which may have introduced some bias to results concluded here.

Low fall survivorship in the north basin documented throughout both years of this study may be due to multiple factors related to differences in thermal habitat gradients across the basins. Low fall survivorship across the north basin may be correlated with increased north-south movement in the fall; changes in water temperature in the fall may promote the movement of walleye southward, allowing them to occupy waters closer to optimal temperatures for a longer duration of time. However, this behaviour may increase individual mortality through commercial fishing activity (September 1st) open season across the lake. Fish would likely move earlier in the fall across the north basin due to the earlier decline in temperatures. This movement may subject some individuals to must pass through the narrow channel area at Doghead Point in order to access the southern basin, which may increase their risk to fishing mortality. This difference in timing between the onset of cooler temperatures between the north and south basins of Lake Winnipeg, combined with the observed occurrence of peak inter-basin movement during the fall in a north to south direction may help to explain some of the additional mortality documented across the north basin in the fall. Further investigation into the timing of north to south movement of walleye during the fall, as well as the degree to which walleye movement is driven by spatial thermal gradients (Raby et al., 2018) may aid fisheries managers in determining the timing of walleye movements and therefore better predict particular time periods and locations in the lake where vulnerability to commercial harvest is highest (and therefore potentially require more carefully regulated management).

Considering both historical and contemporary datasets, between 1–8% of fish moved between basins, indicating that the majority of tagged fish remained within their basin of tagging origin, a behaviour known as partial migration (Bronmark et al., 2013; Chapman et al., 2011, 2012). Partial migration may be an adaptive strategy evolving over time, when migration provides benefits such as increased body growth, survival, and reproduction, typically as a result of improved energy acquisition, ultimately influencing an individual’s life history (Bowlby et al., 2011; Bronmark et al., 2013; Roff, 1988). Partial migration in walleye populations is not uncommon and has been documented elsewhere, though in greater proportions. Across Lake Huron, 57% of tagged walleye remained resident to Saginaw Bay(Hayden et al., 2014) whereas in Black Bay, Lake Superior, 34% of walleye remained resident (Mckee, 2018). The greater distances across the basins in Lake Winnipeg compared to these other systems may explain the lower observed proportions of fish movement between the south or north basins of Lake Winnipeg. Additionally, the weighted receiver gate system which assigned a basin location to fish on a weekly basis in the current study was biased towards the south basin due to wider receiver spacing and overall less coverage in the north basin. Furthermore, influences related to differences in receiver range coverage between basins may have further biased the ability of the gate arrays to detect individuals consistently across the two years of the study.

Though we experienced limitations with both datasets fitting multi-state live-dead mark recapture models in our study, we are confident in the general patterns in walleye inter-basin movement and survival reported here. The historical dataset was composed of only two events for each fish; an initial capture and a final recapture, with no re-sight information between these events. Both the historical and contemporary datasets also consisted of relatively small sample sizes of both tagged and recaptured dead individuals when compared to that of other studies completed using live-dead recapture models (Cowen et al., 2009; Duriez et al., 2009; Kendall et al., 2006). We believe that both of these limitations led to our inability to determine accurate historical survival estimates. We further fitted the historical data to both dead recovery and joint live-dead recovery models to attempt to derive better estimates of survival, however, these models generated similar survival estimates as the live-dead models used here.

Furthermore, we recognize that general bias exists related to commercial fishing activity across the historical dataset, in that dead recaptures were only reported by commercial fishing activity which was likely restricted to areas within a relative distance to harbours as well as during open seasons of fishing. Additionally, as the historical data was reliant upon recaptures via the commercial fishery (varying sizes of gill nets across the lake), results of size effect and inter-basin movement noted across this study are likely bias and should be interpreted with caution.

Ultimately, a clearer understanding of walleye movement across Lake Winnipeg may allow for better management of the resource (Ogburn et al., 2017). Understanding these processes may aid in determining how fish are affected when undergoing future stressors related to a changing climate where thermal maximum temperatures increase, and seasonal variation may be drastic from year to year. Here, we have demonstrated similarly low movements of walleye between the north and south basins of Lake Winnipeg comparing studies conducted over 50 years apart. We have also demonstrated that contemporary walleye movement and survival vary seasonally, with movement being greater in a south to north direction across both historical and contemporary studies. Our data suggest that differences in the timing of movement and seasonal habitat use, combined with a universal season opening in the fall fishery and longer south basins spring and summer fishery may lead to compounded vulnerability to exploitation for individuals. Inter-basin prey density along with an updated assessment of walleye diet across the basins particularly during key summer forage periods may prove valuable in further uncovering survivorship and drivers related to inter-basin movement across the lake. Future work investigating walleye movement in this lake should investigate combining movement results such as those reported here with genetic and metabolic data, which may begin to determine if differences in movement translate into inherited or physiological differences ultimately related to growth or reproductive investments, all of which are important driving factors of individual fitness.

2.6 Acknowledgements

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2.7 Tables and figures

Table 2.1 Historical tag and recapture values for each year of the study across basins. N = number of individuals tagged, n = number of individuals reported captured with associated locations via commercial fishery.

	Year 1	Year 2	Year 3	Across study
N	South: 429 North: 1714	South: 1489 North: 4368	0	South: 1918 North: 6082
n	169	387	171	South: 234 North: 584

Table 1.2 Acoustic telemetry tagging numbers across north and south basins of Lake Winnipeg along with sex of tagged individuals. Tagging locations in Figure 2.1.

	South	North
Spring 2017	170 (Female = 157, Male = 13)	28 (Female= 20, Male=8)
Fall 2017	6 (Female=5, 1 unknown)	0
Spring 2018	72 (Female=37, Male=30, 5 unknown)	82 (Female= 53, Male=7, 22 unknown)

Table 2.2 Top five models from historical tag-based movement study using multi-state live-dead mark recapture models. ϕ= survival, p= resight, ψ= movement, r= reporting rate, Npar= number of parameters in model.

ϕ	p	ψ	r	Npar	AICc	ΔAICc	AIC weight
Constant	Year	Basin	Basin	8	20745.53	0.000	0.47
Year	Year	Basin	Basin	10	20746.58	1.04	0.28
Constant	Year	Year	Basin	9	20747.84	2.31	0.14
Year	Year	Year	Basin	11	20748.73	3.19	0.009
Year	Basin	Basin	Basin	9	20789.15	43.6	1.6e-10

Table 2.3 Top 2 models from contemporary telemetry-based movement study using multi-state live-dead mark recapture models. Symbols as in Table 2.2.

ϕ	p	ψ	r	Npar	AICc	ΔAICc	weight
Basin *Season	Basin	Basin *Season	Basin	40	19397.66	0.000	0.99
Basin *Season	Basin	Basin +Season	Basin	32	19414.13	16.47	2.6e-4

Table 2.4 Historical model and corrected movement estimates annually and across the duration of the study. $\hat{\phi}$ = Independent survival calculation determined using equations 5 through 8 (see methods). $\hat{\psi}$ = annual historical movement corrected for tag losses.

	Year 1	Year 2	Year 3
Model Annual ψ	0.2%	0.9%	0.3%
Corrected Annual $\hat{\psi}$	0.3%	1.2%	0.4%
Independent Annual $\hat{\phi}$	47%	66%	51%

Figures

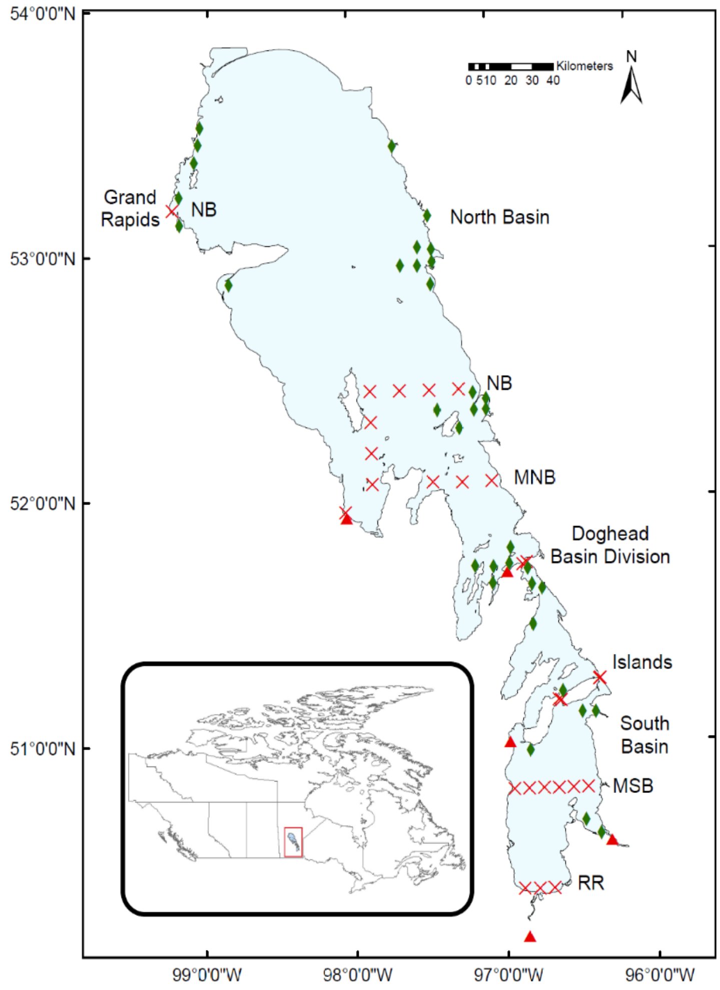

Fig. 2.1. Map of study area with insert to highlight study location within Canada. Acoustic receiver gates denoted by red X's: RR – Red River (3 receivers), MSB – mid south basin (6), Islands – Hecla and Black islands, Doghead Point (North-South division; 2), MNB – Mid north basin (3), NB – north basin (9). Map also denotes contemporary tagging locations (2017–2018) indicated by red triangles and historical tagging locations denoted by green diamonds.

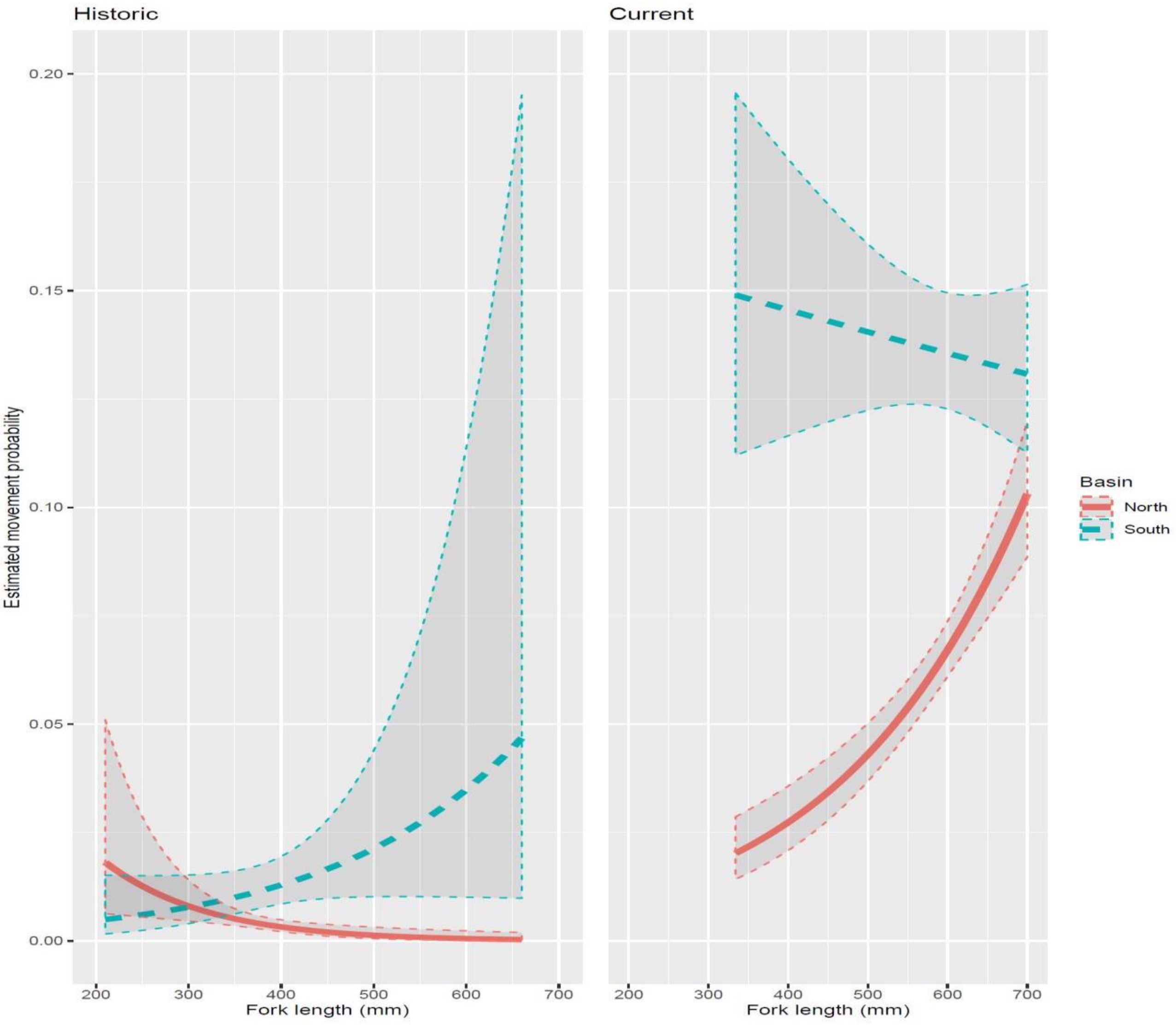

Fig. 2.2. Effect of fork length at size of tagging on estimated movement probability for north basin fish moving south (red, solid line) and south basin fish moving north (blue, dashed line) for both the historical (left) and contemporary (right) movement studies. Confidence intervals (95%) are shown (shaded).

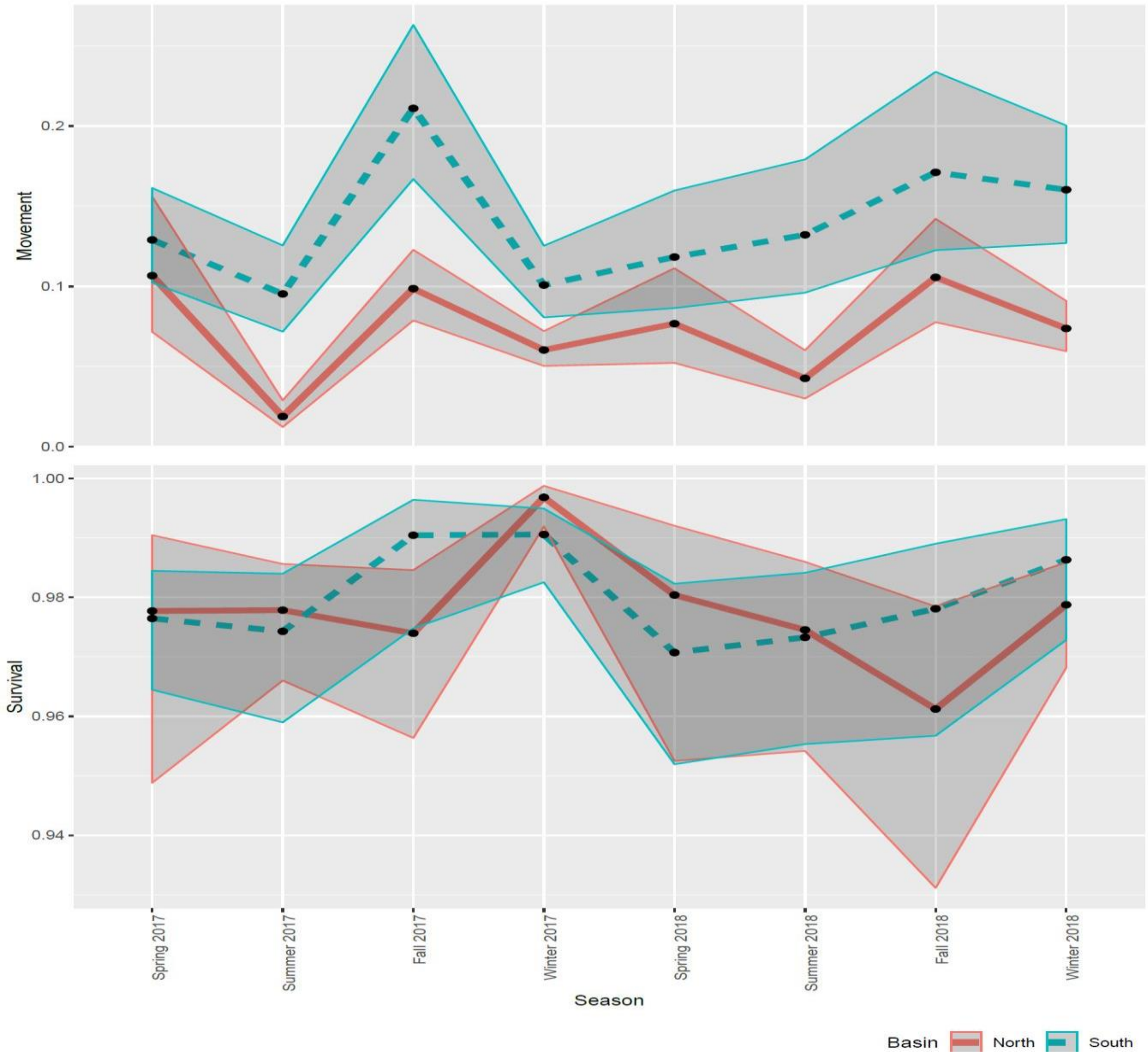

Fig. 2.3. Weekly seasonal movement (top panel) and survival (bottom panel) probability for each basin from spring 2017 to winter 2018. South basin movement estimates are seasonal movement into the north basin in a given season (blue, dashed line), and north basin movement estimates are movement into the south basin in a given season (red, solid line). Confidence intervals (95%) are shown in grey.

Chapter 3. Distinct patterns of movement in seasonal space use suggest differences in putative reproductive success of mature female walleye within Lake Winnipeg (*Sander vitreus*)

3.1 Abstract

Lake Winnipeg hosts North America's second largest walleye (*Sander vitreus*) commercial fishery and is of significant economical value to the province of Manitoba. Spatially, Lake Winnipeg consists of two relatively separate basins differing in both abiotic and biotic features. Currently, little is known regarding how walleye distribute themselves seasonally across the lake. Here, I identify and describe differences in seasonal space use of large mature female walleye across two different strategies of movement (migrant & resident) using data from an acoustic telemetry survey. Walleye were tagged across the south basin of Lake Winnipeg during the spring of 2017 (n= 176), though only a portion of these individuals remained in the study over the two-years of observation (n= 51). Individuals surviving over both years were categorized into groups as either resident (n=18, those remaining below Doghead Point in the south basin where they were tagged), migratory (n=31; walleye that moved above Doghead Point into the north basin), and other (n=2; fish that demonstrated both migratory and resident movement over the 2 year period of study). I used kernel density estimators to determine 95% home range (HR) and 50% core range (CR) polygons and associated centroid locations for each individual walleye across seasons over two years. I found significant differences in HR, CR, and latitudinal location between resident and migrant fishes during the summer and fall seasons. I documented significant differences in migrant HR and CR across seasons, where summer and fall ranges were significantly

greater than in spring and winter. Further, the latitudinal location for HR and CR demonstrated that migratory walleye moved to northern latitudes during the summer and fall and returned to southern latitudes during the winter and spring, when these seasonal ranges overlapped those of residents. Within the Red River, I also documented a greater number of putative repeat spawners among migrants compared with residents. This study is the first to describe two clearly distinct movement strategies across large mature female walleye in south basin, which are also associated with differences in spawning attempts. Further, I present evidence to suggest that the evolution of these alternate movement behaviours is likely a consequence of habitat heterogeneity across the lake, particularly across thermal and prey density gradients.

3.2 Introduction

Understanding fish movement patterns of highly mobile fishes can be critical to the application of effective fisheries management, especially in large freshwater lakes, but is often not considered. Understanding the life history requirements for species, such as preferred habitats for foraging and reproduction, home and core ranges, and differential behaviour patterns among individuals may provide researchers and managers with valuable insight which can lead to the implementation of best management practices (Cooke et al., 2013). For instance, partial migration is a relatively common phenomenon where a portion of individuals in a population demonstrate large home ranges compared with others who remain relatively resident to a particular areas or habitat typically across their entire lifespan (Chapman et al., 2011; Jonsson & Jonsson, 1993; Mueller & Fagan, 2008). Partial migration has been previously documented in freshwater fishes and has been found to be relatively common, particularity across large, heterogenous habitats (Lucas & Baras, 2000; Mueller & Fagan, 2008).

The evolution of different life history strategies within a single species is likely a response to multiple factors that occur across heterogeneous habitats as are commonly found in large lakes; across the Laurentian Great Lakes, acoustic telemetry studies have confirmed both partial and long distance migration behaviours in walleye populations (*Sander vitreus*) that were previously unknown or unconfirmed (Hayden et al., 2017, 2019; Mckee, 2018; Raby et al., 2018; Wang et al., 2007). Partial migration observed across these systems is likely related to individuals' attempts to maximize their fitness by exploiting variable resource availability in space that may provide them with benefits such as increased growth, increased reproductive success, or both (Roff, 1988). These studies have led to new insights regarding potential drivers related to long-range movement; proposed drivers include maintaining optimal temperatures and pursuit of prey densities required to impart greater fitness through increased reproductive opportunities. Long-range migrating walleye movements in Lake Erie and Huron have been previously described to move into cooler, deeper waters following spring spawning, presumably due to behavioural thermoregulation (Peat et al., 2015; Raby et al., 2018; Wang et al., 2007). In Lake Ontario and Superior, larger mature walleye have been found to move out into deeper cooler waters in pursuit of large-bodied or highly energetic prey species (Bowlby & Hoyle, 2011; Hoyle et al., 2017; Mckee, 2018). Further, growth and maximum size were elevated in migratory individuals in Lake Superior (Mckee, 2018).

Lake Winnipeg walleye are an ecologically important species as a native top predator and provide significant economic benefits to the province of Manitoba, providing both sustenance and economic support to Indigenous communities that surround Lake Winnipeg while additionally providing hundreds of jobs directly and indirectly related to commercial and recreational fishing (Conservation Manitoba, 2017; Heuring, 1993; Nicholson, 2007; Probe Reserach, 2018). Recently, both walleye total harvest and relative body condition have declined in response to multiple factors, including deteriorating water quality, an increasing frequency of species invasions and over harvest (Environment Canada & Manitoba Water Stewardship, 2011; Schindler et al., 2012). Over the past decade, harvest rates have more than doubled above estimated maximum sustainable yield for walleye, while reductions in mesh net sizes across the upper half of the south basin and throughout the north basin have resulted in increased capture rates of smaller individuals across Lake Winnipeg (Manitoba Sustainable Development, 2019; Nicholson, 2007). Differences in fishing pressure also exist between the basins, with the majority of fishing effort being concentrated in the south basin (Franzin et al., 2003). Additionally, zebra mussels (*Dreissena polymorpha*) have established across the south basin since 2013 (Enders, 2019), and may be expected to affect walleye production (Geisler, 2015). Similar threats across the Great Lakes historically have led to the collapse of many active and productive walleye fisheries (Schneider & Leach, 1977), raising concern for the future sustainability of Lake Winnipeg walleye populations.

Several studies have investigated morphological and genetic differences across Lake Winnipeg walleye and have found differing conclusions as to whether or not populations in the north and south mix, or remain in their respective basins of the lake (Backhouse-James et al., 2012; Johnston et al., 2012; Thorstensen et al., 2020; Watkinson & Gillis, 2005). Johnston et al., (2012) demonstrated a south to north increase in mean age and size across walleye, and Watkinson et al., (2005) effectively showed distinct differences in scale wavelet analysis between south and north basin fish. However, recent genetic studies have concluded that there was little to no genetic divergence across various sampled spawning locations throughout the lake (Backhouse-James et al., 2012). Following up with this study, RNA sequencing was able to detect gene flow predominantly in a south to north gradient (Thorstensen et al., 2020). Low but measurable rates of movement have been observed to occur between the basins for at least the past 50 years (Chapter 2). Additionally, fish were documented moving between the basins at rates that differed seasonally (Chapter 2). In this chapter, I further address movement on a fine scale seasonal basis, focusing on mature south basin tagged female walleye and will contextualize and quantify these movements across what appear to be identified as two distinct movement patterns of fish spawning in the south basin.

The main objective of this study was to describe the repeatability and seasonal patterns of walleye movement across the south basin of Lake Winnipeg. I assessed the repeatability of movement behaviour by first categorizing individuals into two main groups: residents or migrants, maximum northward distance achieved within a single year. Residents subsequently remained across the south basin while migrants recorded south and northern (Doghead point or above) detections within a one-year timeframe. I then determined home and core ranges for each tagged individual for each season over a two-year period, as well as seasonal latitudinal centroids for each group in each season, and contrasted patterns between groups. Additionally, I evaluated repeat spawning differences among residents and migrants. I hypothesized that residents would demonstrate a greater rate of repeat spawning and body condition given the higher prey density across the south basin (Lumb et al., 2012, 2018), less energy spent travelling long distances, and reduced energy expenditure relative to migrants (Roff, 1988). As well, I hypothesized that residents and migrants would occupy the greatest space (km^2; home and core range) use during the fall when individuals seek out warmer bay and river areas in pursuit of schooling prey and may move in response to cooling thermal gradients (Bowlby & Hoyle, 2011). I also predicted that the most southern latitudinal location for both groups would occur during the spring when walleye moved back to their original tagging locations across the lower portion of the south basin to presumably spawn.

3.3 Methods

Location

Lake Winnipeg (Manitoba, Canada) is the 11th largest lake in the world and can be subdivided into two relatively distinct basins connected by an intermediate channel area. This channel area includes a narrow pinch point approximately 2 km in width. For the purposes of this study, I used this pinch point as a convenient marker to denote the movement of fish tagged in the south basin into the north basin, thus defining them as migrants. This allowed for a higher probability of detection (~90% in 2017, ~70% in 2018, see details below) for fish crossing the Doghead pinch point area. The north and south basins differ in both biotic and abiotic features such as differing maximum summer water temperatures, turbidity, forage prey species and the densities in which they are present, overall depth, and total surface area. In addition to this, delays in ice on ice off events of up to two weeks are typical between the basins due to the four degrees of latitude covered by the lake (Fig. 3.1; Brunskill et al., 1980).

Receivers

A grid style array (Kraus et al., 2018) was deployed across Lake Winnipeg during the 2016 field season, prior to tagging. During 2016, 69 (VR2W, VR2Tx, 69 kHz; Vemco) receivers were deployed across Lake Winnipeg covering the south basin from the Red River to Hecla and Black Island (Fig. 3.1). An additional three receivers were deployed and spaced evenly between the 2 km pinch point located at Doghead. However, the middle receiver at the channel of Doghead point was lost in 2018, resulting in the decline in detection coverage noted above. Receivers were spaced across the lower portion of the south basin in a five km grid, and from the middle of the south basin up to Hecla and Black Island at a seven km spacing (Fig. 3.1). During the 2017 field season, an additional 14 (VR2W, VR2Tx, 69 kHz; Vemco) receivers were added to the middle of the south basin to provide additional coverage (first week of June 2017; Fig. 3.1). Twenty-one (VR2W and VR2Tx, 69 kHz; Vemco) receivers were deployed north of Hecla and Black Island arranged across the same grid with seven km separating each (last week of May 2017; Fig. 3.1). An additional 25 (VR2W, VR2Tx, 69 kHz; Vemco) receivers were deployed north of Doghead point along the grid array and were separated by 14 km (last week of June 2017). A single receiver was deployed at the mouth of Saskatchewan River (May 24th, 2017) while two were placed in the Dauphin River (one at the mouth and 1 km up stream; May 31st, 2017) to record any movement in and out of these larger river systems (Fig. 3.1).

Fish tagging

Walleye were tagged in 2017 across the south basin of Lake Winnipeg. Tagging at the Red River (May 2nd-4th; n=110; female=106, male=4) and Sandy Bar (May 9th-16th;

n=60; female=51, male=9) took place during the spring and an additional tagging effort at the Winnipeg River (October 16th-19th; n=6; female=5, unknown=1) occurred during the fall. All fish captured were fitted with V16 acoustic telemetry tags (VEMCO, Halifax). Acoustic transmitter tags had a nominal random delay range of 85-165 s to ensure equal probabilities at each random delay and to also reduce the probability of transmitter collisions on receivers. Detailed tagging methods have been discussed and ca be found in the methods section of Chapter 2.

Data filtering and management

Raw detection data were filtered to remove any false detections (Pincock, 2012). Using these filtered data, I plotted each tagged individual using abacus plots to filter out fish that may have experienced tag failure, dropped a tag, or may have been removed from the study as a consequence of harvest. If individuals were not detected again after entering the north basin, they were also removed as I could not determine if they experienced mortality or had permanently emigrated into the north basin beyond receiver coverage. After assessing which individuals remained alive over the duration of the study (May 15th, 2017 – March 31st, 2019; n=51), clear patterns of movement behaviour became evident. All receivers within the south and north basin were grouped as a single functioning unit to determine the maximum extent an individual may have achieved within a given year. Migratory fish were defined as individuals that recorded both south and north (movement passed at or past Doghead Point) locations across a given year, repeatable over two years, while resident fish were categorized as individuals that remained south of Doghead point for the entire duration of the study period. We recorded two individuals as ‘others’ who demonstrated varied movement patterns where they did not demonstrate repeatability (i.e. migrant one-year, resident the next), and these two individuals were dropped from further analysis. After grouping individuals, I had a total of 31 migrants and 18 residents (Table 3.1).

To compare putative repeat spawning between the groups, abacus plots of female walleye tagged in 2017 in the Red River were used. Red River females were used as they were initially tagged during spawning, and spawning status at the time of capture and tagging was recorded. Individuals recorded on any receiver within the Red River during the following spring (2018) were assumed to be present to spawn (Fig. 3.2).

Center of Activity (COA) was determined for individual walleye using the VTrack (Dwyer et al., 2018) package in the R statistical environment (R Core Team, 2019; Simpfendorfer et al., 2002). The COA incorporates detection data from multiple receivers across the array which is then translated into a single weighted mean position based across a specified bin of time (Simpfendorfer et al., 2002). As I had already determined that a subset of walleye were moving large distances (see above), I opted to use a 1 hr time interval which has been previously suggested for use in relatively active and mobile species (Brooks et al., 2019; Simpfendorfer et al., 2002). Hourly COA locations were then used to determine seasonal home range, core range, and associated mean centroid locations.

Seasonal time bins included summer (June 15th – August 31st), fall (September 1st – November 15th), winter (November 16th – March 31st), and spring (April 1st – June 14th;

2018 only) across both 2017 and 2018. Data from both 2017 and 2018 were included, but the varied timing of walleye tagging excluded any useable data from spring of 2017. Removing spring 2017 detections from the analysis allowed for individuals to fully mix back into the population and resume normal behaviour following tagging (Wilson et al., 2017). Seasons were determined by water temperature data, which triggers known biological meaningful events across walleye, such as spawning and fall runs (Fig. 3.3). Individual estimates for home range and core range for each season in 2017 and 2018 was calculated using the Kernel Utilization Distribution (KUD; ‘href’ smoothing parameter) from the “adehabitatHR” R package (Calenge, 2006). A minimum number of unique COA positions (5) is required to calculate the home range and core range of an individual within a given season. This was not always the case across our dataset and occurred across several migratory individuals who recorded <5 unique COA locations in the north basin due to a lack of receiver coverage. This also occurred in both migratory and resident individuals during the winter season when individual activity levels dramatically decreased (see results). These individuals may have moved above the reach of the grid array, went undetected due to the greater distance between the receivers, or experienced tag collisions due to the high number of fish tagged in the south basin (walleye and other species). Polygons of home range and core range were created for each season using the KUD estimate. Each individual KUD polygon was then clipped to a spatially referenced polygon to fit within Lake Winnipeg (Fig 3.1; Charles et al., 2017; Gutowsky et al., 2015), excluding islands and surrounding land. Polygon values for each season were obtained in km^2 and the mean centroid location from each KUD clipped polygon were also recorded to assess latitudinal differences in movement.

Detection efficiency

This study used a grid-style array in order to document both fine and large-scale individual movement (Kraus et al., 2018). The array offered different coverage dependent on where an individual may have been spatiotemporally located relative to receivers on the grid. High coverage exists across the lower portion of the south basin within the 5 km grid, but lowest in the northern 14 km grid, leaving an individual more likely to go undetected in the northern basin (Kraus et al., 2018). As a result, I expect that the home range, core range and associated mean centroid locations of migratory individuals were likely conservative due to differences in receiver spacing across the lake. This is particularly likely to have occurred during the summer and fall seasons when migratory walleye were documented moving into the north basin and when I additionally noted that a large portion of migratory walleye went undetected during the summer months. In addition, some seasonal and annual variation in detection efficiency across the lake does exist that could further bias home and core ranges estimates, and all should be considered when interpreting results presented here.

Detection efficiency varied both seasonally and annually from 2016 to 2017, with detection efficiency declining during some seasons and with respective distance from the receiver (Appendix F). Detection across the winter season was highest and relatively constant likely due to factors related to ice coverage (i.e., no noise generation from wave action and decreased turbidity; Appendix F).

At the narrow basin division (Doghead), not all receivers originally deployed were retained over the course of the two-year study. During 2017, all three receivers were present and deployed across the 2 km channel with the middle receiver deployed off centre, spaced 1.5 km and 0.5 km from the two opposite receivers close to the shoreline. Therefore, if an individual moved between two receivers on one side of the channel spaced 1.5 km apart, at maximum that individual would be 750 m away from detection on any receiver. The detection probability at this distance (although variable with season as previously discussed) was typically found to be ~80% (C. Charles, Personal communication). Consequently, if an individual moved between the middle of the opposing receivers spaced 0.5 km apart it could be within 250 m of either receiver, allowing for a ~96% detection range probability (C. Charles, Personal communication). However, during 2018, the middle receiver at Doghead point was lost, leaving the two remaining receivers close to the shoreline and spaced ~2 km apart from one another. This meant that individuals could have been a maximum distance of 1000 m from either receiver at any given time, if passing directly between the two.

Analyses

I calculated condition (K) for each individually tagged fish (n=175) using Fulton's condition factor $K = 100\frac{W}{L^3}$. First, I first assessed if a relationship existed between fork length and condition by plotting the data of all tagged fish. I did not find any significant relationship between fork length and body condition at the time of tagging, suggesting no length-related bias in condition estimates, and therefore proceeded with assessing differences in body condition between residents and migrants using a Welch's two sample *t*-test.

I used Generalized Linear Mixed Effects Models (GLMM) to assess seasonal and group (resident & migrant) differences for each year in home and core range use (km^2). Both season and group (resident & migrant) were fixed effects and individual tag animal tag identification was included as a random effect. Estimated latitudinal centroid locations were also evaluated using GLMMs as described above.

I assessed the models for normality of residuals and constant variance (Zuur et al., 2009). In order to address issues related to residual heteroscedacsity, I chose to adjust the variance structure of the model. I used the *varIdent* variance structure which allowed for the model to have a different variance for each combination of season and group (i.e., different variance structure for both spring migratory and spring resident groups). I further compared this variance structure to both a fixed and power structure variance, however ΔAICc indicated that all models under the *varIdent* variance structure provided a better fit to the data paired with visual assessments of normality plots. I therefore did not transform the response variable, which has the potential to alter the relationship with the predictor variable (Zuur et al., 2009). All models were fit using the "nlme" R package (Pinheiro et al., 2020). To visually assess relationships between groups and seasons, I plotted the mean covariate prediction value for each season and group with associated 95% confidence intervals for home range, core ranges, home range latitude, and core range latitude, controlling for inter-individual differences. To further determine if significant differences existed between groups and/or seasons existed, I used the ‘multcomp’ (Bretz et al., 2020) package in R to run Tukey-type pairwise comparisons.

3.4 Results

Of the 31 walleye categorized as migrants, 20 were subsequently tagged during the first year of the study spawning across the Red River. As for individuals categorized as residents (n=18) 15 were tagged during the spring spawn across the Red River. Only individuals tagged during the spring across the Red River were assessed for repeat spawning activity in the following year. Based on individual abacus plots, I documented 13 of 20 walleye identified as migrants (65%) that re-entered the Red River in 2018 which were originally tagged during 2017, suggestive of repeat spawning. By contrast, only 6 of 15 walleye identified as resident (40%) and tagged in the Red River re-entered the Red River in spring 2018. After log transforming the condition (K) data to address issues with normality, I found no significant differences in body condition between residents and migrants (t-0.955, df=58.76, p=0.3433).

I then compared the significance of both additive and interactive effects using log-likelihood model comparisons in R with the anova() function across all four GLMM (home range, core range, home range centroid, core range centroid) and found that in all comparisons, the model with the interaction term always explained more variation than the additive models (p=<0.001). Therefore, all models were interpreted at the level of the interaction between season and group (resident and migrant).

Home Range (95%) and latitude centroid

Home range space use revealed significant differences between summer ($p < 0.001$) and fall ($p < 0.001$) across the groups while spring ($p = 0.988$) and winter ($p = 0.340$) space use was similar between migrants and residents (Fig. 3.4). Within the resident group, I documented similar home range estimates across spring, summer, and fall, with winter significantly different from the three other seasons ($p < 0.001$; Fig. 3.4). The greatest mean seasonal home range for residents was recorded during the fall at 1191.5 km^2 (min= 953.1 km^2, max= 1430 km^2) while smallest mean seasonal home range was during the winter at 273.6 km^2 (min= 157.3 km^2, max= 389.9 km^2). Across the migratory group I saw significant differences in space use between fall-spring ($p<0.001$), spring-summer ($p < 0.001$) and summer-winter ($p < 0.001$) while fall-summer ($p = 0.1097$) as well as spring-winter ($p = 0.3968$) home range did not significantly differ from one another (Fig. 3.4). The greatest mean seasonal home range was documented across the fall for migrants at 6818.3 km^2 (min =5904.3 km^2, max= 7732.3 km^2) while, like residents, the smallest mean seasonal home range use was during the winter season at 667 km^2 (min= 315.5 km^2, max= 1018.5 km^2).

Latitudinal centroids of home range locations reflected similar patterns to those of home range space use, indicating that most of the seasonal movement displayed by walleye was along a north-south axis. Mean covariate predictions for latitude centroid locations were significantly different from one another during the fall and summer seasons across migratory and resident groups, while latitudinal distribution of groups was similar across spring and winter seasons (Fig. 3.5; Fig 3.6). For residents, all seasonal latitudinal distributions were similar with no significant differences noted. Mean centroid latitude location was approximately 50.79412 for all seasons across residents (Fig. 3.6). The migrant group demonstrated significant differences in latitudinal location between the fall-spring ($p < 0.001$), spring-summer ($p < 0.001$), and summer-winter ($p < 0.001$) while latitudinal distribution between fall-summer ($p = 1.00$) and spring-winter ($p = 1.00$) were similar and did not significantly differ from one another. The most northern mean seasonal latitudinal home range position for migrants was recorded across the summer months at 51.69963 (min= 51.54067, max= 51.85859) approximately 100 km (straight line measurement) north from the mean spring centroid location (Fig. 3.6). The most southern latitudinal location was during the spring at 50.90037 (min= 50.71065, max= 51.09008).

Core range (50%) and centroid latitude

Core range space use demonstrated similar trends to those documents across 95% home range space use estimates. Between groups, I observed significant differences in core space between the fall ($p < 0.001$) and summer ($p < 0.001$) but not the spring ($p = 0.999$) and winter ($p = 0.469$) seasons (Fig. 3.4). For residents, I noted similar space use across summer-spring ($p=1.00$), summer-fall ($p = 0.1882$), and spring-fall ($p = 0.6004$) with significant differences between winter-summer ($p < 0.001$), winter-spring ($p = 0.0149$), and winter-fall ($p < 0.001$; Fig. 3.4). Greatest mean seasonal core range for residents was documented during the fall (316.3 km^2, min= 236.5 km^2, max= 396.2 km^2) and smallest mean seasonal core range was during the winter (54.5 km^2, min= 24 km^2, max= 85 km^2). For migrants, I noted significant differences between core range space use during fall-spring ($p < 0.001$), spring-summer ($p < 0.001$), and summer-winter ($p < 0.001$) groups with similar core range between fall-summer ($p = 0.4969$) and spring-winter ($p = 0.7630$; Fig. 3.4). The greatest mean seasonal core range for migrants was recorded during the fall (1915.6 km^2, min= 1558.5 km^2, max= 2273.2 km^2), while the smallest mean seasonal core range was during the winter at 136.6 km^2 (min= 56.5 km^2, max= 216.8 km^2).

Core range latitude centroid locations demonstrated similar patterns to those observed for home range estimates. Between groups I documented differences in space use again between fall-summer months with similar core range latitude distribution across the spring-winter months (Fig. 3.5, Fig. 3.6). For residents I did not document any differences in latitudinal distribution across seasons. Average latitude location for all seasons was approximately 50.77932, very similar resident home range latitude. For migrants I documented significant differences between fall-spring ($p < 0.001$), spring-summer ($p < 0.001$), and summer-winter ($p < 0.001$), with no differences between fall-summer ($p = 0.936$) and spring-winter ($p = 0.99$). The most northern latitude recorded for core range was for migrants across the summer months at 51.54103 (min= 51.32646, max= 51.75559) while the most southern latitude for migrants was recorded during the spring at 50.77485 (min= 50.58775, max= 50.96195) separated by approximately 85 km when measured in a straight line.

3.5 Discussion

This study demonstrates clear differences in movement behaviour between resident and migrant walleye, as determined by home and core range estimates as well as clear latitudinal changes in distributions seasonally of migrants (but not residents) over two consecutive years of monitoring. My original hypothesis that residents would demonstrate both a higher rate of repeat spawning and body condition was not supported, as results presented here indicated that migrants were more likely to repeat spawning in the following year and body condition did not differ between groups. Furthermore, a distinct partial migration strategy among south basin walleye was described, which involved repeatable behaviour over two years for both residents and migrants. Home range analysis demonstrated that residents occupied a relatively similar range of space across all seasons considered in the study, with slight but non-significant seasonal variation except during the winter season. Within groups, residents occupied the greatest amount of space during the fall, but the least amount of space in winter months. For migrants, home and core range use was significantly different across seasons (fall-spring, summer-spring, summer-winter, fall-winter), with the largest home range observed during the fall and smallest in the winter. Differences between the groups in home range and core range occurred primarily during the summer and fall seasons and were strikingly different, but also remarkably similar between resident and migrant walleye during winter and spring. The increase in home range space use for migrants during the summer and fall was coupled with a northward shift in latitudinal distribution, indicating that this captures the majority of the directionality of movement for walleye spawning across the south basin. Collectively, these findings provide strong evidence for distinct movement strategies that may reflect differences in putative reproductive success among walleye in the south basin of Lake Winnipeg.

Across estimates of core, home and mean centroid locations, I found significant differences across migratory and resident groups between the summer and fall seasons, where migrants revealed a more northern latitudinal distribution during the summer and fall seasons than migrants. A number of walleye studies have found similar trends in the Laurentian Great Lakes where a portion of the walleye population travelled large distances, while some individuals remained in closer proximity to their tagging locations (Bowlby et al., 2011; Hayden et al., 2014; Hoyle et al., 2017; Mckee, 2018; Peat et al., 2015; Raby et al., 2018; Wang et al., 2007). In multiple studies, walleye movement, migration, or both typically followed spring spawning events and has been speculated to be a response to seeking out rich summer forage areas (Hoyle et al., 2017; Mckee, 2018; Wang et al., 2007) and preferred or optimal water temperatures (Hayden et al., 2014; Peat et al., 2015; Raby et al., 2018; Wang et al., 2007). Lake Winnipeg covers 4° of latitude, which allows for a dramatic temperature gradient along its south-north axis to exist; north basin ice-off events are typically delayed by about two weeks in the spring and occur two weeks earlier in the winter (Brunskill et al., 1980). In addition, the south basin is more shallow, turbid, and warmer, on average, compared to the cooler, clearer, and deeper north basin (Brunskill et al., 1980). Average summer surface water temperatures from 1999 to 2007 were approximately 19.7°C in the north basin and 21.5°C in the south, a difference of nearly 2°C. (Environment Canada & Manitoba Water Stewardship, 2011). Habitat heterogeneity across the basins with respect to temperature, water clarity and depth have likely been present across this lake for thousands of years, and likely has played some role in the development of partial migration patterns in walleye, presumably by affording migrants some advantage over residents, potentially related to growth, condition, fecundity, increased survival, or a combination of these factors (Chapman et al., 2012; Roff, 1988).

Across Lake Erie, research on walleye thermal preferences has demonstrated that individuals who moved across the lake to cooler, deeper waters experienced two peaks in growth (Kershner et al., 1999). Migratory walleye in Lake Erie who moved from the shallower western basin which warms faster then the cooler central basin as temperatures increased were able to take advantage of growth related to temperature in the western basin and additionally as they reached the central basin due to exposure at optimal temperature range for a greater length of time compared to individuals who did not move (Kershner et al., 1999). Walleye spawning throughout the Red River are often able to spawn earlier compared to any other location across the lake due the more rapidly warming water temperatures available here during the spring (Fig. 3.3). Furthermore, though migratory patterns or probability of migration may potentially be related to body size (Chapter 2), I did not document any differences in migratory behaviour associated with body size in the current dataset; it has been hypothesized that larger bodied individuals may seek out cooler water temperatures than is considered within their optimal range (18-22°C; Hokanson, 1977; Lester et al., 2004), while smaller and typically younger individuals may prefer warmer temperatures (Lafrance et al., 2005; Morita et al., 2010). This is because larger bodied individuals can encounter a higher metabolic cost when occupying warmer water temperatures, which, while costly to larger fish may actually be beneficial for smaller bodied individuals

(Morita et al., 2010). Migrant individuals spawning across the south basin may experience benefits related to growth, similar to those documented across walleye in Lake Erie and Huron that moved into cooler areas of the lake during the summer months (Kershner et al., 1999; Peat et al., 2015). As temperatures across the south basin begin to reach upper limits of thermal optimum, migrants in turn may follow this temperature gradient north, occupying cooler and potentially more optimal temperatures related to growth. Furthermore, the majority of migrants were documented moving back into the south basin during the early winter when their latitudinal distribution was documented to be similar and overlapping with that of residents. This could indicate that migrants may also follow water temperature gradients south as north basin waters begins to cool earlier across the fall season, allowing migrant walleye to continue to remain in closer to optimal thermal habitat, subsequently increasing their overall growth, fecundity, or both.

Overwintering latitude between the two groups was similar and there were no significant differences between migrants and residents during the winter months. In addition, both migratory and resident groups demonstrated the greatest reduction in home and core space use during winter. Based on very similar estimates of mean latitudinal centroid location, home range and core range during the winter months, resident and migrant walleye occupied very similar winter habitats (Fig. 3.6). Trawl survey data has demonstrated that forage prey density and availability is higher across the south basin (Lumb et al., 2018). The south basin may be able to sufficiently support walleye during winter forage activities which allow them to also reduce their overall space use, conserving energy during the winter months. Winter foraging and habitat can be critical in order for walleye to survive and successfully spawn during the following spring. During the winter months, walleye continue to replenish and build visceral fat stores necessary for successful spawning (Henderson et al., 1995). Additionally, while initially investigating the detection data of walleye to determine the fate of each individual and general movement patterns, walleye appeared to overwinter within close proximity to known spawning locations (Red River). Although mean centroid locations place walleye in the center of the south basin (Fig. 3.6), this is likely due to the larger temporal resolution associated with the seasonal time bins. Overwintering (winter) and spawning (spring) latitude location across the models for home and core range within groups did not significantly differ from one another, confirming this original observation across the dataset that resident and migrant walleye may stage themselves during winter for quick access to spring spawning areas.

Although I did not find any differences related to body condition at the time of tagging between the two groups, it does not discount other differences in reproductive output or somatic cell growth differences that may exist between residents and migrants. Once walleye reach a relatively large size and become mature (as were the individuals tagged across our study population), additional energy acquired typically is directed to reproductive growth (Henderson et al., 1995). Differences between resident (40%) and migrant (65%) walleye in putative repeat spawning activity observed in the Red River, a known and active spawning location, may be due to differences in resource availability between the two groups. Energy acquisition following the spring spawn is important for walleye as they need to restore visceral fat levels that are essential for reproductive output (Henderson et al., 1995). Henderson et al., (1995) found that the switch to diverting energy into reproductive output in walleye likely occurs around August and September and continues through the winter until the following spring spawn event. If an individual was not able to replenish fat stores during the summer and fall months, it was highly probable that an individual would be more likely to skip spawning in the following year (Henderson et al., 1995).

Residents and migrants differed in mean latitudinal locations during key feeding seasons (summer and fall). Discrepancies in the number of repeat spawning individuals documented across the Red River demonstrate support that migrants may express a benefit associated with reproductive fecundity over their resident counterparts. In addition, walleye typically demonstrate relatively high but potentially variable rates of spawning site fidelity (Hayden et al., 2017; Zhao et al., 2011). To date, studies into spawning site fidelity across Lake Winnipeg have not been investigated. However, Hayden et al. (2017) looked at spawning site fidelity across lakes Huron and Erie, concluding that Lake Huron walleye demonstrated high fidelity (95%), while Lake Erie walleye were somewhat lower (70%). In the south basin of Lake Winnipeg, and in particular in the Red River where I looked at repeat spawning behaviour, spawning walleye may take advantage of preferable spawning habitat here related to the Red Rivers warmer spring water temperatures and generally decent spawning habitat (appropriate spawning substrate, turbidity levels, flow rates). These factors may motivate migratory individuals to return in the winter in order to continue foraging and stage prior to spring spawning which may increase spawning site fidelity behaviour here. The observation of a higher proportion of migrants returning to spawn suggests that a migratory behavioural strategy may provide additional energy needed to support repeat spawning compared to south basin residents. Though migration can be a costly behaviour, it can prove beneficial (Rennie et al,. 2012). Further analysis into egg fatty acid profiles, reproductive, and muscle tissue analysis between the two groups are key next steps to investigate possible differences in fecundity and energy density differences.

There were no differences associated condition between residents and migrants, which may be related to the slightly larger mean fork length of residents at time of tagging (migrants= 609.26 mm, residents= 619.55 mm). Typically studies that have focused on size-based movement have found that larger bodied individuals are more likely to move further then smaller bodied individuals due to the higher metabolic cost associated with migration (Chapman et al., 2012; Roff, 1988). Condition is often closely related to prey availability (Liao et al., 1995; Rennie & Verdon, 2008), so it might be expected to be higher in migrants if afforded some net positive benefit associated with forage prey density. However, given that both a greater number of migrators were present across all surviving individuals included in this study, and that migrators were more likely to repeat spawning activity compared with residents, this collectively suggests that migratory individuals may encounter some benefit residents do not. In Great Lakes lake whitefish (*Coregonus clupeaformis*) populations, individuals that demonstrated the greatest home ranges also displayed the highest growth and consumption rates (Rennie et al., 2012). Although both groups of walleye in the current study demonstrated large fork length sizes at the time of tagging, further investigation into growth patterns of these individuals could determine if migrants do demonstrate increased growth rates, as might be predicted from other research. This has been demonstrated in a population of tagged walleye across Black Bay, Lake Superior where migrants demonstrated an increased growth rate/maximum size over their resident counterparts (Mckee, 2018). It may be possible that migrants are able to access or encounter additional productive habitats across the lake which in turn offset the energetic costs required to travel longer distances.

The existence of partial migration combined with spawning suggests some foraging advantage for migrants, though this is inconsistent with known prey distribution and densities across the lake (Lumb et al. 2018). However, prey density must be considered within other aspects of predator foraging, such as detection and reaction distances which are often related to water clarity, even for walleye which are low-light adapted predators (Lester et al., 2004). Thus, increased visibility in the north basin could allow for greater foraging success despite higher prey densities in the south. Optimal water clarity measured for walleye sits around 2 m (Lester et al., 2004). Average annual secchi depths measured from 1999 to 2007 varied between 0.66 m and 2.13 m across the north basin and 0.3 m to 0.76 m in the south basin (Environment Canada & Manitoba Water Stewardship, 2011). In addition, the lake experiences seasonal variation in turbidity levels where the south basin experiences increased turbidity during the summer and fall (<0.7 m), compared to that of the north basin (~1.5 m; Environment

Canada & Manitoba Water Stewardship, 2011). Differences in turbidity levels, particularly across the summer and fall when walleye were documented moving into the north basin may also be related to declines in thermal-optical habitat area (TOHA) across the south basin. Reduced TOHA during key feeding seasons may outweigh benefits associated with greater prey density found across trawl survey data throughout the south basin (Lumb et al., 2018). Furthermore, pockets of prey may exist across the deepest areas of the channel and north basin (32m and 18m) where cisco, a cold-water species may take refuge during the summer months allowing walleye easy access to this prey species. Additionally, stable isotope analyses could be used to help determine if differences in forage prey species between the two groups exist (e.g., Hobson, 1999). Differences between prey size, prey energy density, and detection/ foraging success related to TOHA may be able to be further help explain the observed migratory behaviour of walleye observed here.

Several fish (56) that moved into the north basin across this study eventually went undetected and were last observed in the north basin, suggesting either mortality (natural/harvest) or straying. Additionally, four migrants remained in the north basin after migrating in the early summer (2017) and remained across the north basin for the winter and following spring seasons. These individuals may have spawned across the north basin during the following spring (2018). These four fish were then documented migrating back to the south basin either during the late fall or early winter (2018) of the following year. Since these four individuals moved from the south to north and north to south in both 2017 and 2018, they were categorized as migrants. Due to the lack of receiver coverage across the north basin, once an individual moved out of receiver range, I was unable to determine if a fish simply went undetected or experienced some form of mortality. This rate of disappearance (31.8%, or 56/176 tagged fish) across the north basin and that I additionally documented four migrants that overwintered and spent the following spring-summer across the north basin gives some indication that straying, partial immigration or some combination of both is present. As such, south basin fish may represent a metapopulation, providing a significant source of fish and genetic material to the north basin. Straying or partial immigration into the north basin would also correspond with recent genomic and genetic findings which demonstrate a subtle south to north direction in the transmission of genetic material (Backhouse-James & Docker, 2012; Thorstensen et al., 2020). Further investigation by expanding the receiver array into the north basin to better understand whether fish emigrate into the upper half of the north basin as mature and or immature individuals as well as if both males and females demonstrate this behaviour would be required to further understand the dynamics that may be occurring across the lake.

Facultative migration was found in only six fish across this study, whereas the majority (45) displayed repeatable patterns of behaviour. Two out of 51 individuals who survived across two years of this study displayed variability in their movement behaviour and four of the 51 individuals demonstrated partial immigration to the north basin. This effectively demonstrated that not all individuals across the south basin can necessarily be categorized as a migrant or resident, and that while this behaviour was repeatable for the majority of fish considered in this study, migratory behaviour may be facultative for some. Similarly low rates of facultative migratory behaviour in walleye have been reported elsewhere (Mckee, 2018).Partial migration may develop across a population for a number of different reasons and may be a learned behaviour, fixed through an individuals experiences during early conditions, or alternate depending on environmental cues (Chapman et al., 2011). Further investigation would be required to determine if other patterns of movement exist and what ultimately drives these movement patterns and behaviours.

Based on results presented here, the north basin walleye population is clearly made up of south basin spawning individuals for at least a portion of the year. This key finding should influence how the north and south basin walleye populations are managed both across the recreational and commercial fisheries. A strong spawning population of walleye across the south basin, in particular the Red River, likely contributes to a greater population of walleye across the north basin, especially during the summer and fall seasons then has been previously considered. Understanding how the south and north basins are connected and the subsequent links between the density of each basin should prove valuable in developing best management practices. Expanding our understanding of north basin spawning individuals and their subsequent movement behaviour will complement work completed here on south basin spawning stocks. Additionally, investigating the distribution and movement pattern of immature and smaller bodied individuals (males), that are at an increased vulnerability to capture by commercial gear (due to their smaller size) may additionally provide further insight to management.

Limitations

Over the two year duration of this study, fish appeared to experience high mortality, emigration or both; of the fish tagged during 2017 across the south basin (n=176), only 51 individuals survived or otherwise remained detected on the grid over the course of this two-year study. Other individuals were either harvested across the north and south basin (this scenario is likely, given the intense demand of the recreational and commercial fisheries), experienced natural mortality, or disappeared (emigration) across the north basin. I was therefore limited by a small sample size of 51 individuals (49 in the models) which greatly restricted model selection in order to ensure a high degree of reliability and fit while maintaining sufficient degrees of freedom. Future work might consider including additional individuals tagged in future years (e.g., those tagged in 2018) who survived for at minimum one year or longer to additionally inform home and core range estimates. The 2018 tagging effort incorporated a greater diversity of tag sizes due to the use of a smaller tag sizes (V13) which aided in the capture of male individuals spawning across the Red River. This could allow for future models to additionally consider a size at tagging, sex effect, or both across the GLMM in order to address how this may influence best model fits.

Detection efficiency typically changes on a seasonal basis and can be influenced by many different environmental factors (Binder et al., 2016; Kessel et al., 2014). Detection appeared to be lowest during the fall into winter and the summer (Appendix F) when I demonstrated increased movement across the migrant group. This may have led to weaker detection efficiencies which could have negatively biased the COAs and kernel density estimates of home, core range, and associated centroid locations. I likely captured relatively accurate estimates of resident home and core ranges given the detailed receiver coverage across the south basin. However migratory space use during the summer and fall was likely underestimated as movement up into the north basin with increased spacing between receivers and lack of coverage across the north basin would have allowed for some individuals to go undetected for a longer time period than fish that remained in the south (as home and core range estimates were derived from COA locations which required at least 5 unique locations). Therefore, core and home range estimates are likely conservative, but are still able to provide us with insight into how individuals move across the lake given that estimates are on the order of thousands of km and 1° of latitude for migrant walleye. Furthermore, receivers were deployed north of Doghead Point during the last week of June 2017 following the spring tagging event in the Red River. The summer seasonal time bin incorporated any movement between June 15th- August 31st, 2017. It therefore may have been possible for a fish tagged during the beginning of May across the south basin to have moved up into the north basin before June 15th prior to receiver deployment. This would have negatively impacted the summer home and core range estimates for migrants during 2017.

Conclusion

I found that large female walleye tagged across the south basin of Lake Winnipeg demonstrated two clearly different patterns of movement behaviour, where migratory individuals typically travelled north in the early summer and returned south during early winter, additionally these behaviours were repeatable over two years of observation.

Heterogeneity between the north and south basins in terms of commercial and recreational fishing pressure, temperature, turbidity, and forage prey densities have likely played a role in the development of these different movement patterns. Furthermore, I uncovered evidence that is suggestive of being associated with life history differences (higher occurrence of repeat spawning across migrants). Future investigation into additional possible benefits (e.g. growth, other measures of reproductive output) and potential mechanisms that support migration (diet, foraging success, thermal conditions that may result increased energetic efficiency, TOHA) and differentiate these fish from residents should be addressed to better understand the drivers of movement in some individuals (or lack thereof in others). In addition, results described here should be followed up to identify if migratory and resident differ at the molecular level (e.g., genetic and metabolomic differences), which may help to further understand the variation in movement behaviour described here. It may also be reasonable to further describe home and core range of walleye on a finer temporal scale (e.g., monthly or bi-weekly basis) across the summer and fall to gain a greater understanding of overall habitat use within seasons while addressing fine scale temporal resolution to best pinpoint when long distance migration occurs.

3.6 Tables and Figures

Table 3.1. Tagging information for migrant and resident individuals that survived for the two-year duration of the study. See Fig 3.1 for tagging locations.

	Sex	Mean FL at tagging (mm)	FL range at tagging (mm)	Tagging location
Migrant	1 Male 30 Female	609.26	Min 480 Max 721	11 Sandy Bar 20 Red River
Resident	1 Male 17 Female	613.7	Min 453 Max 706	1 Winnipeg river 2 Sandy Bar 15 Red River

Figures

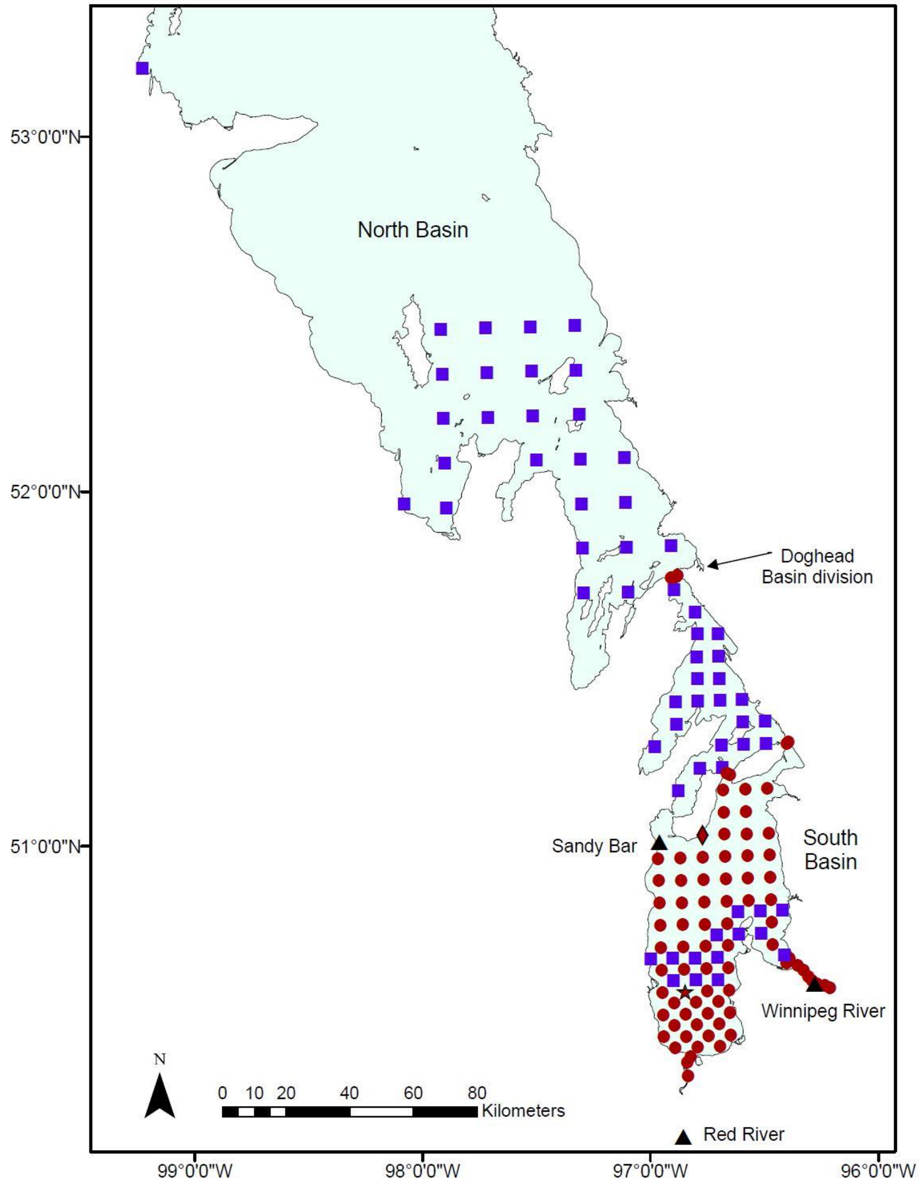

Fig. 3.1. Map of the study location. Basin division at Doghead point with receiver deployment over 2016 (red circles) and 2017 (purple squares). Additionally, the map depicts three tagging locations (Red River, Sandy Bar, Winnipeg River) across the south basin indicated by black triangles, reference tag location (red star; Appendix F. Fig. F3), Lake Winnipeg temperature data logger location (red diamond; Fig. 3.3), and the Red River temperature data logger (black triangle; Fig 3.3).

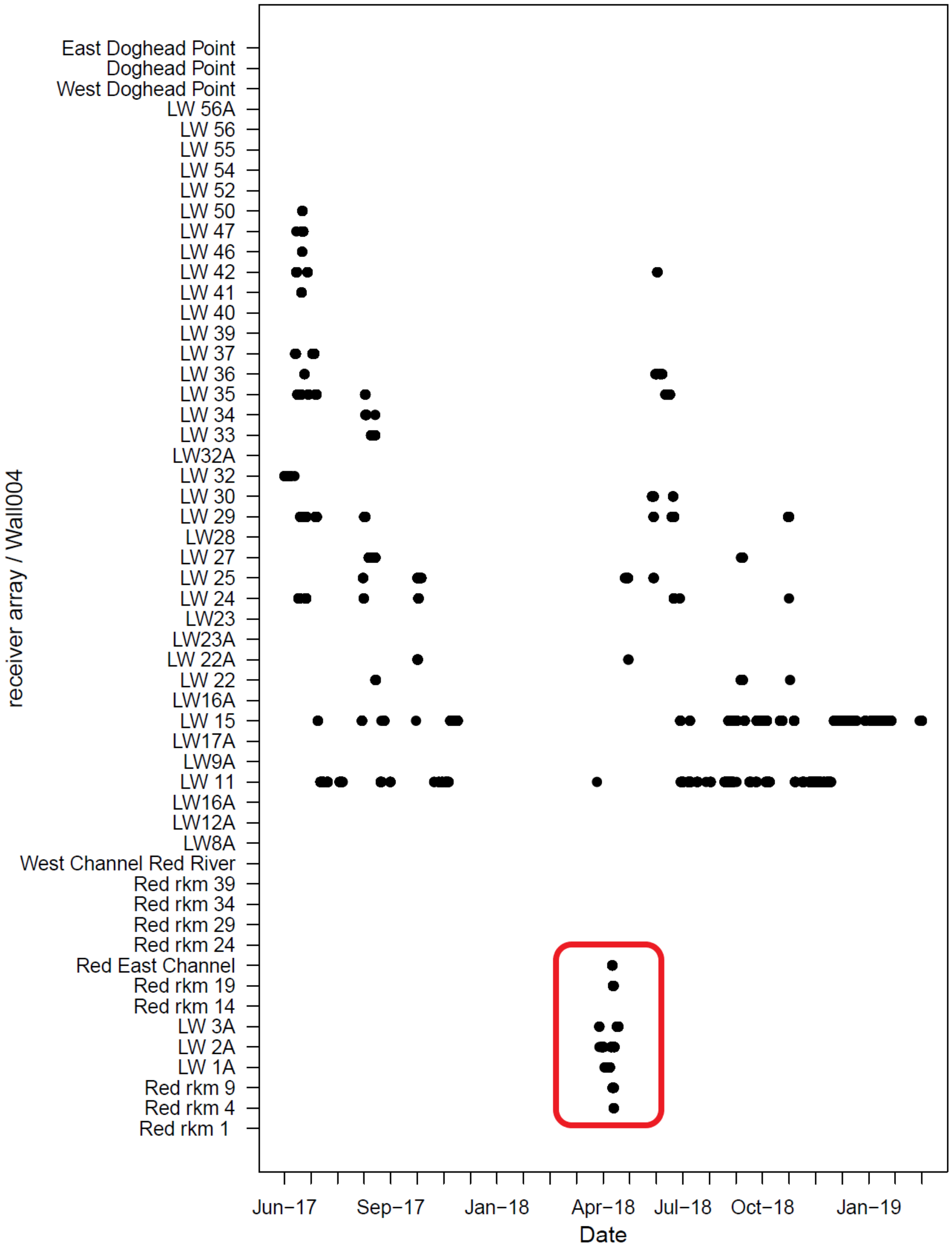

Fig. 3.2. Abacus plots of wall-004 (resident), all receiver locations are below Doghead point and fully within the south basin of Lake Winnipeg. Red box indicates that the individual attempted spawning the following spring (2018) as it was recorded within the Red River during the appropriate spawning time frame. Receivers listed from north (top) to south (bottom) in relative order.

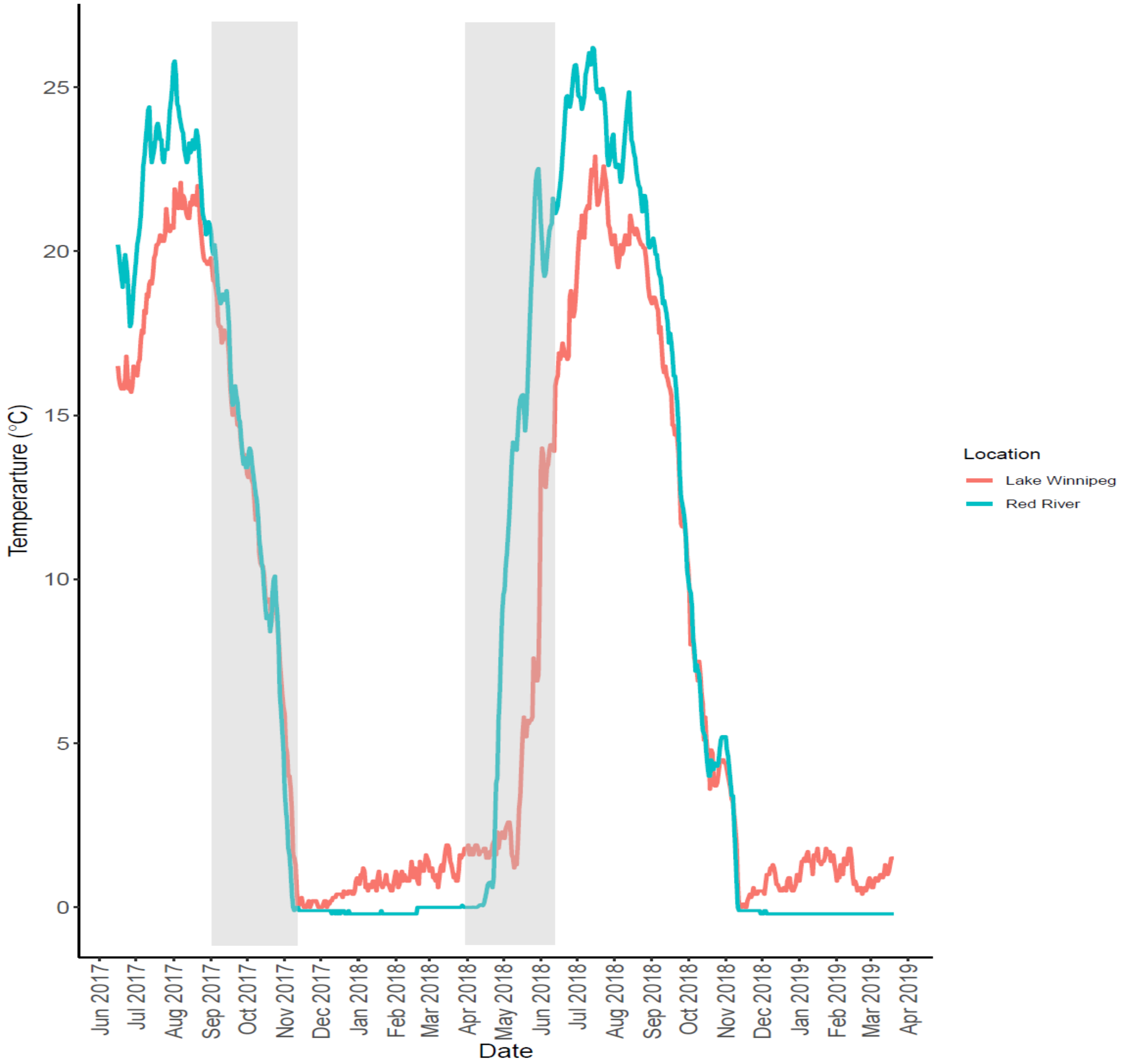

Fig. 3.3. Temperature profile of Lake Winnipeg and the Red River over the course of the two-year study. First shaded grey bar indicates the Fall 2017 seasonal time bin, second shaded grey bar indicates the spring 2018 seasonal time bin. Lake Winnipeg and Red River temperature logger indicated on Fig. 3.1.

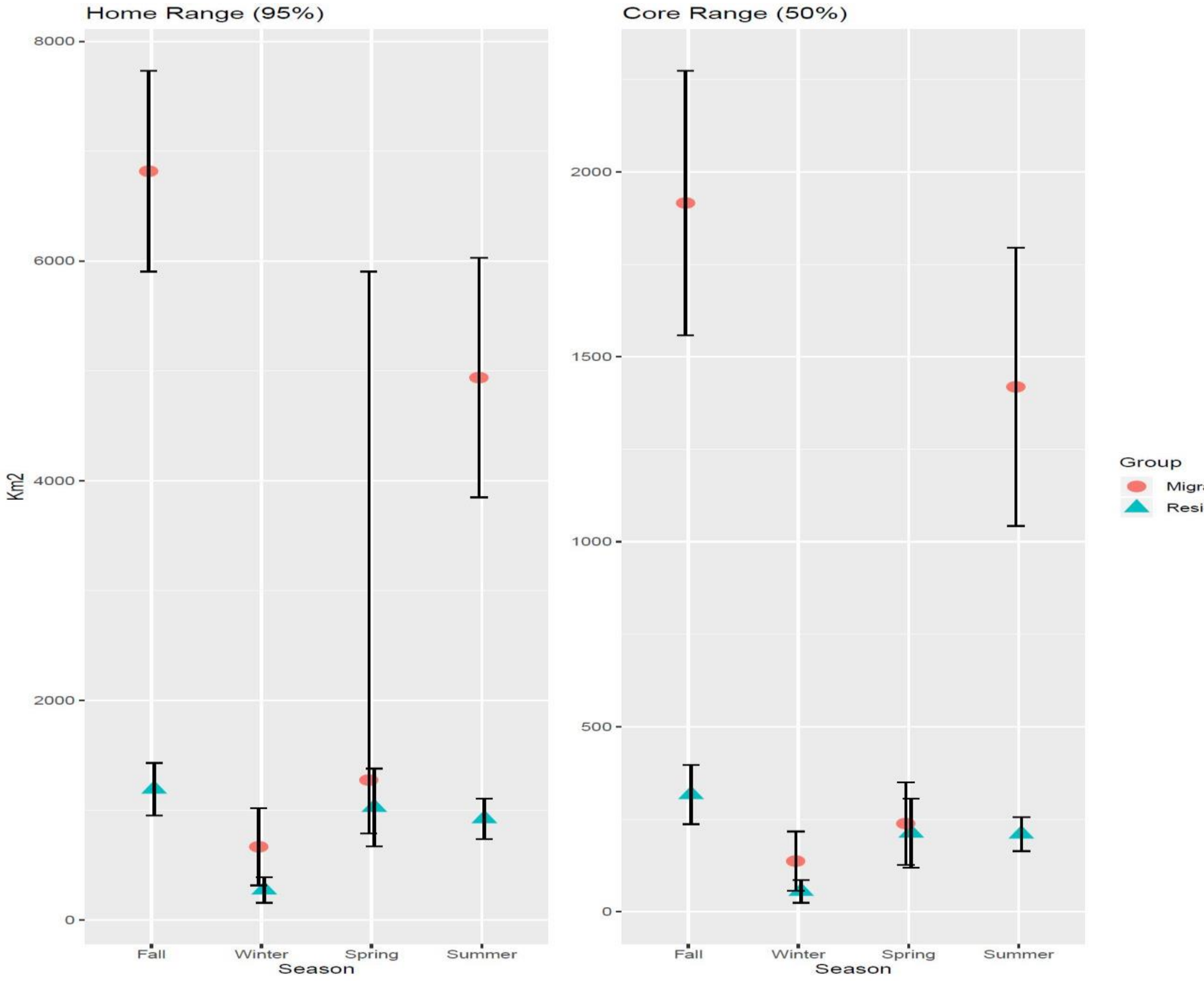

Fig. 3.4. Mean 95% home range and 50% core range values (km2) from the generalized mixed effects models. Error bars around the mean values demonstrate upper and lower 95% mean confidence intervals around the estimates. Large confidence intervals around migratory individuals during the spring likely captured fish were moving large distances prior to the end of this time seasonal time bin.

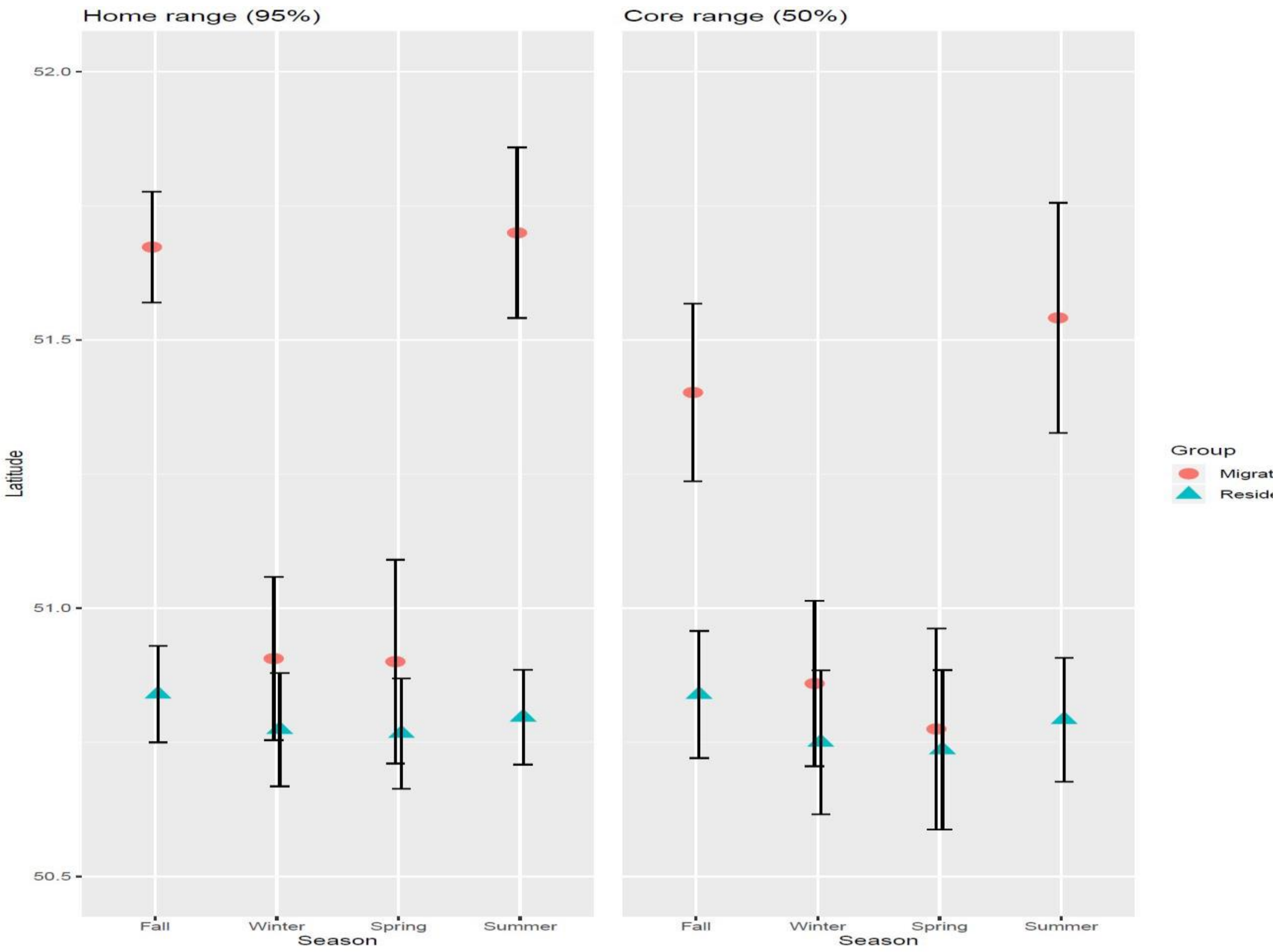

Fig. 3.5. 95% home range and 50% core range mean latitudinal centroid from the generalized mixed effects model derived from home and core range kernel density estimates. Mean centroid locations for home and core range are plotted on fig 3.6 to visualize differences in north south movement between groups and seasons.

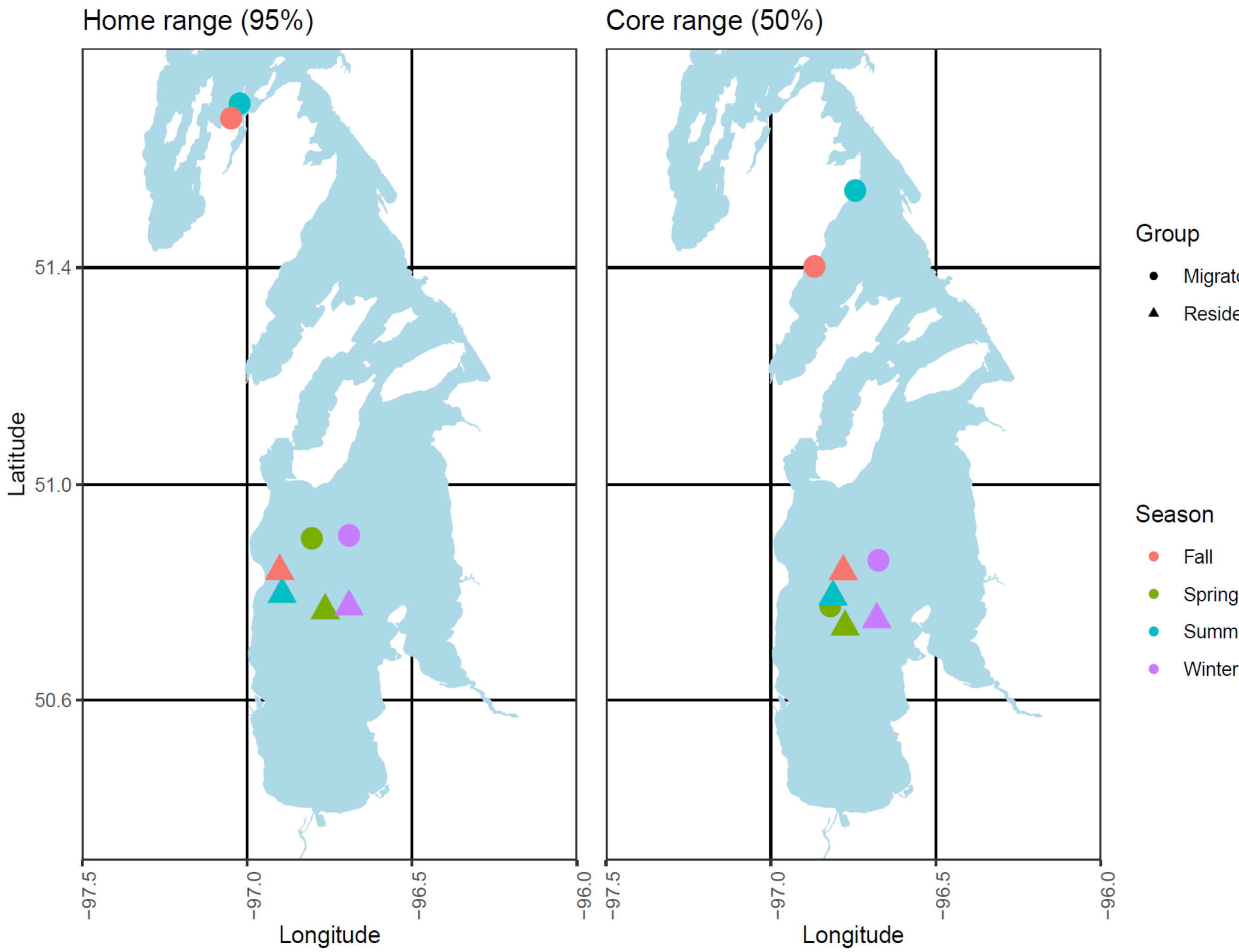

Fig. 3.6. Map of 95% seasonal home range and 50% core range mean centroid locations derived from kernel density polygons and generalized mixed effects model. 50% core range migratory summer centroid estimates have been moved longitudinally to fall within the lake boundary.

Chapter 4. Conclusion

Direct measurements of movement across fishes can provide scientists and resource managers with a greater understanding of how a species uses its surrounding environment and how movement might change over spatial and temporal scales. Further, through direct measurements of movement, we can begin to classify patterns of behaviour and formulate hypotheses to investigate the environmental drivers related to these behaviours. Ultimately, this will allow for a greater understanding of the variation observed in life history strategies within species. This can be of importance across a species that is also a natural resource and can provide managers and policy makers with critical information in developing the most appropriate science-based regulations to allow policy and regulations to take movement patterns into account. Incorporating movement information collected by acoustic telemetry studies may appear in the form of stock-specific management (different quotas and net mesh sizes across different areas of the lake), identifying critical habitat for future restoration or permanent and partial closures. Finally, these management suggestions may further be used to address issues related to increased mortality across spatial and temporal scales of Lake Winnipeg that were documented across this thesis (Chapter 2).

Throughout this study, I demonstrated that a portion of walleye tagged during the 1970s as well as presently use both the south and the north basins of Lake Winnipeg. Further investigation into the contemporary acoustic telemetry data revealed that south basin spawning walleye demonstrated two different behaviours of movement (categorized as resident and migrant). Differences in movement across the lake, specifically those documented across the south basin are likely related to changes in seasonality linked to water temperature gradients, forage prey densities and distribution, water clarity (prey detection), commercial and recreational fishing pressure, and subsequent walleye abundance across the lake. My study is the first to provide direct evidence of inter-basin movement for walleye across Lake Winnipeg and additionally demonstrates that this behaviour has been present for at least 50 years.

Results from the second Chapter provide some support that movement and body size may be correlated. In Chapter 2 I used the entire population of tagged walleye over both years (2017/2018) and was able to detect slight differences in movement patterns across basins associated with body size; specifically, I demonstrated that smaller bodied individuals were more likely to move from the south to north basin whereas it was larger individuals that tended to move north to south. However, throughout the third Chapter, I did not detect any differences between migrant and residents when assessing body condition. I expected a difference related to body condition, size, or both, as previous research has demonstrated that smaller bodied individuals are less likely then larger bodied individuals to travel large distances within a given year (Roff, 1988). However, this could have been due several different reasons, including a small sample size of fish utilized in the second Chapter and a tagged population that consisted of only large females, a consequence of the large size of tags used in the 2017 tagging effort (V16 tags used only). However, this work should be followed up using the wider range of fish sizes tagged in 2018 to better determine if there is in fact a relationship between condition (and body size) as this could provide valuable information to Lake Winnipeg's size-selective fishery.

In the third Chapter of the thesis I documented differences across the number of individuals that repeated spawning activity the year after tagging between resident and migrant groups. An in-depth look into Red River spawning site fidelity would further be required to validate the preliminary results on spawning presented here. If migrants do in fact demonstrate an increase in growth, especially early growth rates, perhaps derived through back-calculations of ageing structures (scales are available for most tagged fish during 2017, scales and spines for fish tagged in 2018), this may provide additional evidence of an energetic benefit to migration (Henderson et al, 1995). These results warrant further investigation to better determine if differences in reproductive output are present between the groups. Reproductive output could be measured though determining the length at first maturity (Froese & Binohlan, 2000), gonadosomatic indices (GSI), or by looking at fatty acid profiles of ovary lipid content across individuals.

I suspect that migratory walleye are primarily driven to move to the north in response to changing water temperatures which can be below sub-optimal in the south basin particularly for larger bodied individuals as south basin spawning walleye were documented across the north basin during the summer and fall months. Migratory walleye may be driven to return to the south basin to spawn within the Red River the following spring. The Red River is a highly productive spawning location, bringing the warmest waters into Lake Winnipeg following winter. This can allow walleye to spawn up to a month earlier compared with any other location across the lake (E Enders., Personal Communication). Migratory walleye therefore may in fact demonstrate high spawning site fidelity to the Red River as they are driven to return from their summer and fall migration north to the south basin primarily to spawn. The Red River may be a potential area to focus future restoration efforts (water quality and habitat improvements) or even be closed (sanctuary) to recreational fishing for a portion of the year throughout the spring.

Using Cormack -Jolly-Seber mark-recapture models, I was able to determine across both historical and current datasets that walleye were more likely to move northward from the south basin. Across the third Chapter I additionally concluded that individuals moving in a south to north direction had dramatically increased home and core ranges space use during the summer and fall seasons compared to those who remained in the southern basin. Results presented across this thesis effectively demonstrate that a proportion of the walleye population does in fact mix across the lake. Documented ecological specialization between north and south basin walleye is likely a reflection of resident individuals and potentially influenced by sampling time and duration (Johnston et al., 2012; Sheppard et al., 2018; Watkinson & Gillis, 2005). Although I was not able to demonstrate that a straying behaviour was present, I did conclude that 56 Of 176 individuals tagged in 2017 were last detected in the north basin at some point throughout the two-year study. Additionally, in the third Chapter I was not able to categorize two individuals as resident or migrant because they did not demonstrate a repeatable movement behaviour. This provides some indication that other patterns of movement likely exist and movement across some individuals may be facultative and is not necessarily repeatable (potentially biologically or ecologically dependent), or both. This may offer some support that individuals tagged in the south basin do demonstrate some rate of straying, whether it be partial or permanent immigration to the north basin. This would support recent genetic and genomic studies that have demonstrated a south to north drift in walleye genetics across the lake (Backhouse-James & Docker, 2012; Thorstensen et al., 2020).

Current research that has focused on migration across fish populations has typically found that large-bodied individuals are more likely to travel long distances as they are better able to account for the additional expenditure of energy (Roff, 1988). Furthermore, migration typically provides some form of benefit related to survival, growth, fecundity, or a combination of these (Chapman et al., 2012; Roff, 1988). This work demonstrated (Chapter 2) size-based movement may in fact be present across the system. However, contrary to current research I observed smaller bodied individuals moving from south to north. It may be probable that smaller south basin walleye are more likely to migrate into the north basin as it provides some benefit related to 1) reduce intraspecific competition across the south basin and 2) optimal water temperatures related to increased body size, fecundity, or both, by following temperature gradients north-south and south-north with seasonal change. Additionally, smaller bodied individuals travelling north may return to the south basin after they have reached a larger body size (as I demonstrated large bodied individuals moving north-south in Chapter 2), remain within the north basin permanently (stray), or demonstrate the migratory behaviour documented during the third Chapter. Additional investigation would be required to further assess factors related to body size, condition, and age to determine if biological characteristics influenced fish movement behaviour.

It is likely the development of migrant and resident behaviour across south basin spawning walleye populations has developed over a long period of time. Differences in movement strategy may have developed due to major abiotic and biotic differences between the two basins. These differences across the lake have likely motivated walleye to exploit various pockets of habitat to obtain some benefit related to growth, fecundity, or both. As the lake continues to experience stressors (invasive species introduction, changing climate, anthropogenic influences etc.), rates at which walleye demonstrate either movement behaviour strategy likely will alter over time in reflection of the changing ecosystem. As seasonal summer water temperatures rise due to climate related changes, south and north basin thermal maximum temperatures will also experience increases (Environment Canada & Manitoba Water Stewardship, 2011). If the movement of south basin walleye is currently driven by thermal temperature gradients across basins, the number of individuals moving south to north may increase significantly. As south basin water temperatures begin to reach upper limits, particularly for larger bodied individuals, the north basin may act as a summer and fall thermal refuge habitat. Additionally, if north basin walleye are making south basin migrations (at a reduced rate), this behaviour may also disappear due to the increase in summer water temperatures. Ensuring the proper management of this stock, in particular the large female walleye moving south to north and north to south with seasonal change would prove essential as these fish likely contribute to a large majority of spawning effort across the south basin during the spring (Red River) as well as the north basin population during the summer and fall months. Understanding these patterns and the drivers motivating movement could allow for a stock-specific management approach which would incorporate knowledge demonstrated across this thesis to ensure various movement behaviours are not at an increased risk of exploitation and inevitably extinction from the system.

4.1 Future research

This work has been the first to describe the spatial ecology and distribution of walleye across Lake Winnipeg. Although I was able to present relevant and new findings that may aid fisheries management and future conservation efforts, I was also left with many unanswered questions. Further investigation into both mature males and immature walleye should provide a more detailed analysis of how various age classes and sex may differ across movement behaviour. Further, investigating male and immature walleye may provide additional answers for determining the drivers and motivation of walleye to travel long distances or remain within a relatively small range. This may assist our overall understanding of different movement strategies across the lake and further assist management and conservation.

An investigation into determining how and if migrant and residents differ in growth rates, reproductive output, and diet may aid in furthering our overall understanding of these two groups. I documented a greater number of migrant individuals versus that of residents during the third Chapter analysis, this was determined by including only individuals that survived across two years of the study. Success across groups could be determined through an individuals ability to survive, as only a surviving individual is able to make the decision to move in the following year (Brodersen et al., 2014). Therefore, across my analysis migrants may in fact be more successful strategy. If migrants are in fact more successful, further investigation into differences related to growth may provide additional answers. This could also be followed up with carbon and nitrogen stable isotope analysis to determine if difference in diet and food web connectivity exist. Walleye diet compositions between the north and south basins have been found to differ, with walleye in the north basin consuming primarily a piscivorous diet and south basin walleye including a combination of fish and benthic invertebrates (Sheppard et al., 2015). Determining if differences in stable isotopes exist and its relationship to growth rates may provide scientists and management with some additional insight into how migrants and residents differ across their overall success (survival, growth, fecundity).

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Appendices

Appendix A

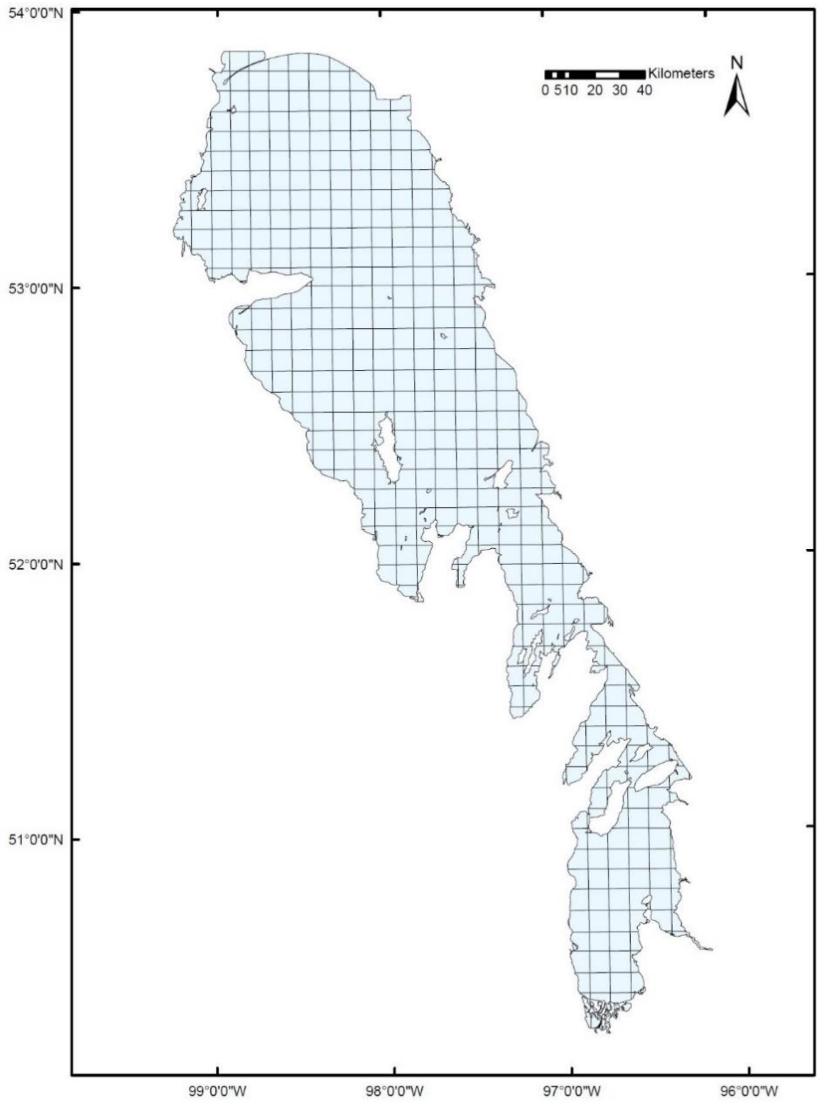

Fig. A1. Lake Winnipeg with historical grid style overlay that was used to record both fish tagged initially as well as fish captured through the commercial fishery. Each grid is approximately 8.5 by 8.5 km. The grid is labelled 1–49 in a north to south orientation and A–Z in a west to east orientation.

Appendix B

Spacing between receiver gates and receiver gate lines used in the contemporary analysis

The distance from the Red River receiver gate to the mid south basin gate was approximately 46 km while receiver spacing between the mid south basin gate was approximately 7 km. The distance between the mid south basin and island (Hecla and Black) receivers was approximately 40 km. Distance covered between the island receiver gates and Doghead Point was approximately 63 km. Distance separating the Doghead Point receiver gate and the mid north basin receiver line was approximately 40 km with receivers in this gate spaced 14 km apart from one another. Distance between the mid north basin line and the north basin line was approximately 40 km with receivers spaced approximately 14 km except for one receiver at Grand Rapids approximately 140 km north of the north basin receiver gate (Fig. 2.1).

Appendix C

Multi-state live-dead mark-recapture model assumptions

Assumptions of this model are as follows; each individual that is marked and present in the population at the time of sampling has the same probability of being recaptured or resighted. Each marked individual has the same probability of surviving until the next sampling period (j+1). Marked individuals are recorded without error and 100% of tags are retained across all individuals for the duration of the study period. Sampling periods are instantaneous, and emigration from a sampled area is permanent. Each individual's fate is independent from that of others. Movement probabilities are equal for all tagged individuals between all basins, and movement probability does not depend on the history of any tagged individual (no memory). Further survival is an estimate of individuals that may have moved off the study location (emigration), been removed and unreported from the study, or died of natural causes in the study and was not reported or documented. (Brownie et al., 1993; Pollock et al., 1990; Seber, 1986).

Appendix D

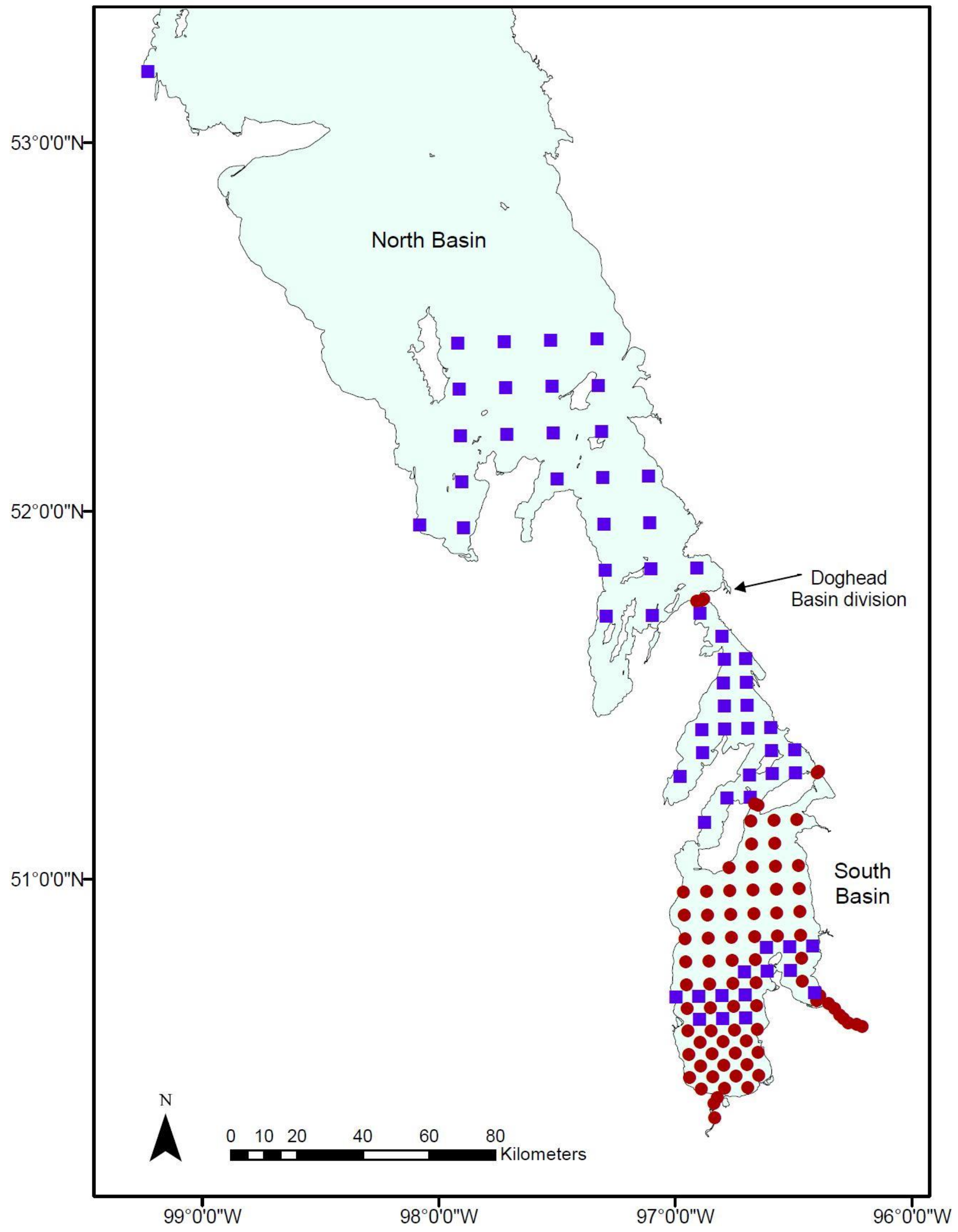

Fig. D2. Full extent of the grid style array deployed across Lake Winnipeg during the study. Receivers south of Doghead were used to determine the fate of an individual to determine the point in time a fish may have been removed or died within the study period. Red circles indicate receivers that were deployed during the 2016 field season while the purple square indicate receiver locations that were deployed the following year during the 2017 field season

Appendix E

Tables demonstrating all possible model comparisons considered in the historic and contemporary data analysis modelling

Table E1. Contemporary model combinations were run and tested against the most general model to determine the most appropriate model fit without overparameterizing any of the model estimates, these fit 36 different possible model combinations (not including the general model).

	Movement (ψ)	Survival (φ)	Resight	Report rate
General model	Stratum*Season	Stratum*Season	Stratum	Stratum
	Stratum+Season	Stratum+Season	Constant	Constant
	Season	Season		

Table E2. Historical Model combinations that were run and tested among the most general model to determine the most appropriate model fit. We attempted to run annual stratum additive and interactive models; however, this was abandoned after determining models were severely overparameterized and did not fit the data appropriately. 36 possible model combinations using the fits shown in the table (not including the general model)

	Movement (ψ)	Survival (φ)	Resight	Report rate
General Model	Annual	Annual	Stratum	Stratum
	Stratum	Stratum	Constant	Constant
	Constant	Constant		

Appendix F

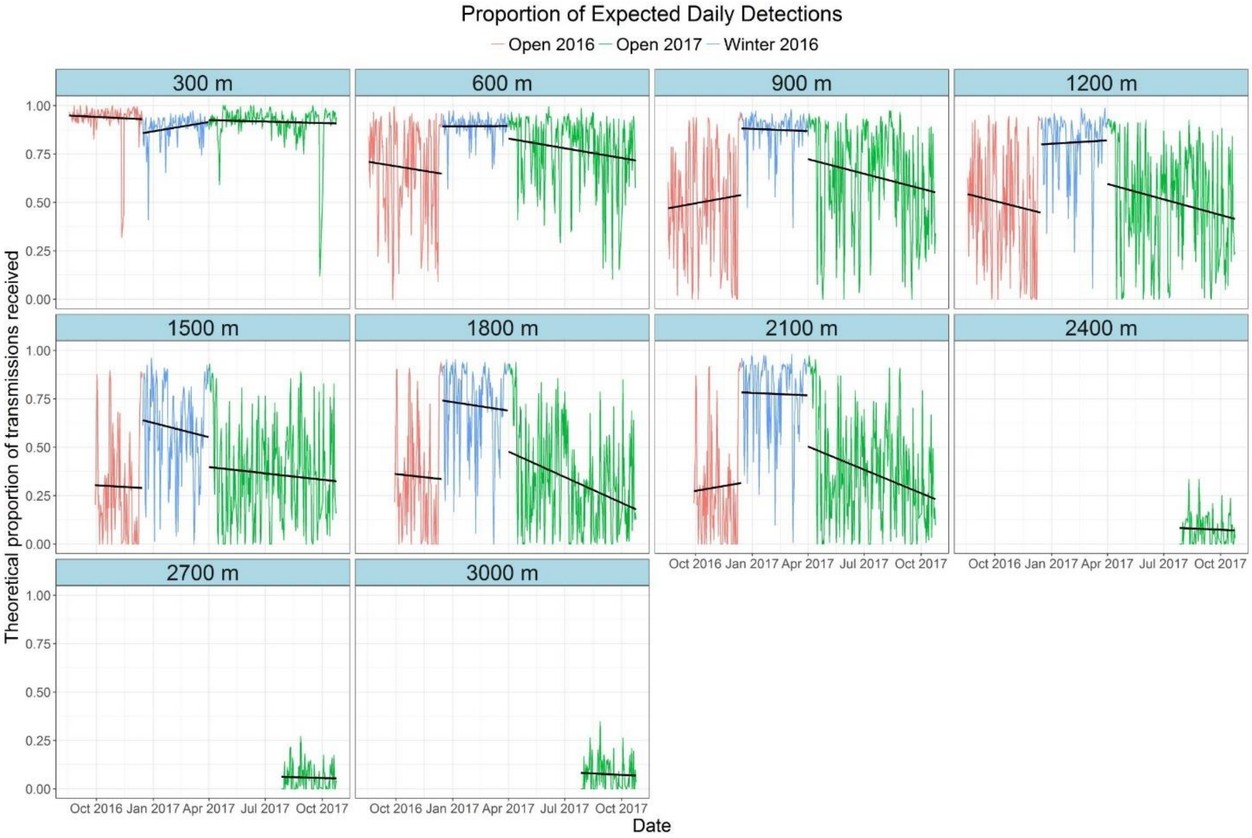

Fig. F3. Seasonal detection efficiency across the south basin of Lake Winnipeg. Receiver location indicated on Figure 3.1 map. Red indicated the open water season in 2016, blue demonstrates the winter season in 2016 to 2017 while green represents the open water season in 2017. Figure made by C. Charles, DFO Freshwater Institute, and reproduced with permission.